OVULES AND SEEDS OF THE POLYGALACEAE

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THE OVULES of the Polygalaceae are anatropous, bitegmic, and crassinucellate, and they frequently have a long exostome (Davis, 1966). The often-hairy seeds contain flattened or thickened cotyledons; the seed coat is endotestal, often in the form of long palisade cells, or is reduced. The larger seeds have a multiplicative testa and an extensive, postchalazal vascularization (Netolitzky, 1926; Corner, 1976). The seeds generally have a mostly white exostome aril that is highly variable in size; the raphal and chalazal regions can be swollen (Chodat, 1890–1893; Blake, 1916; Adema, 1966). The exostome and the swollen chalazal region function as an elaiosome in at least some species of *Polygala* and *Comesperma* (Sernander, 1906; Berg, 1975).

Detailed morphological studies of polygalaceous seeds are scarce (Corner, 1976, *Polygala venenosa* subsp. *pulchra* (Hassk.) Steenis; Rao, 1964, *Salomonia cantoniensis* Lour.; Wirz, 1910, *Epirixanthes*; Verkerke & Bouman, 1980, *Polygala vulgaris* L.; Verkerke, 1984, *Xanthophyllum*). Rodrigue (1893) skillfully compared different seed coats, but minor errors and incomplete material mar her conclusions, which were adapted by later investigators (see also Verkerke, 1984).

The reduction of the mesophyll in the outer integument within *Polygala* (Verkerke & Bouman, 1980) represents a neotenic trend in the development of the ovules and seeds in this genus. In the present study ovule ontogeny and seed development were examined in 14 genera. These new data permit both the elucidation of relationships between genera and a reconstruction of the evolution of polygalaceous seeds. Rodrigue (1893) emphasized the relation between fruit walls and seed coats in the Polygalaceae, and I have compiled a synopsis of fruit characters in order to further taxonomic and morphological studies of the family.

SYNOPSIS OF GENERA AND DESCRIPTION OF THE FRUITS

POLYGALEAE

ATROXIMA Stapf. Lianas or lianalike shrubs; 2 species; western and central Africa. Ovary 3-locular, with 1 epitropous, ventral ovule per locule. Fruit a subglobose, 1- to 3-locular berry, up to 5 × 5 × 4 cm, either smooth and shiny, orange, with mesocarp fleshy and endocarp thin, glossy inside, or pustulate, brown, with mesocarp crustaceous and endocarp thin, glossy inside (Breteler & Smissaert-Houwing, 1977).

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BREDEMEYERA Willd. Climbing shrubs; 50 species; South America. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit an elongated, 2-locular, dehiscent capsule, up to 20 × 7 × 3 mm; pericarp fleshy (Chodat, 1896).

CARPOLOBIA G. Don. Shrubs or treelets, occasionally tall trees; 4 species; tropical Africa. Ovary 3-locular with 1 epitropous, ventral ovule per locule. Fruit a subglobose, 1- to 3-locular berry, 2 × 2.5 × 2.5 cm, smooth, yellow to orange-red at maturity; exocarp thin, mesocarp fleshy, endocarp thin (Breteler & Smissaert-Houwing, 1977; De Koning, 1983).

COMESPERMA[1] Labill. Herbs or climbing shrubs, rarely lianas; 30 species; Australia. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a flattened, often elongated (with the base attenuated), 2-locular, dehiscent capsule, up to 20 × 7 × 3 mm; pericarp membranaceous (Chodat, 1896).

EPIRIXANTHES Blume. Saprophytic annual herbs; 3 species; Indo-Malesia. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a transversely oval, 2-locular berry, not exceeding 4 × 3 × 3 mm; pericarp thin, fleshy (Backer & Bakhuizen van den Brink, 1963).

MONNINA Ruiz & Pavon. Shrubs or perennial herbs, rarely lianas; 160 species; southwestern United States to South America. Ovary mostly 1-locular, with 1 epitropous, ventral ovule. Fruit either a 1-locular samara, up to 12 × 13 × 3 mm, with a hard pericarp, or an elliptic, 1-locular drupe, up to 12 × 6 × 6 mm, smooth, green, with a fleshy mesocarp and a hard endocarp (Wendt, unpubl. ms).

MURALTIA Necker. Prickly shrubs; 115 species; South Africa. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a flattened, 2-locular, dehiscent capsule, up to 5 × 4 × 2 mm, often with 4 spines; pericarp membranaceous (Levyns, 1954).

NYLANDTIA Dumort. Spiny shrub; 1 species; South Africa (Cape). Ovary 1-locular, with 1 epitropous, ventral ovule. Fruit a subglobose, 1-locular drupe, up to 7 × 7 × 7 mm, smooth, first green, ripening red; mesocarp fleshy, endocarp hard (Chodat, 1896; Rice & Compton, 1950).

POLYGALA L. Annual herbs to small trees; over 500 species; almost cosmopolitan. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a flattened, often marginate, 2-locular, dehiscent capsule, from 4 × 2 × 2 mm up to 12 × 13 × 4 mm; pericarp usually membranaceous, sometimes fleshy (Chodat, 1890–1893, 1896).

SALOMONIA Lour. Annual herbs; 3 species; Indo-Malesia, China, and Japan. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a transversely oval to obreniform, 2-locular, dehiscent capsule, not exceeding 3 ×

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[1] Van Steenis (1968) included *Comesperma* in *Bredemeyera*, but the seeds of the two genera are described separately.

4 × 4 mm, with several long spines; pericarp membranaceous (Chodat, 1890–1893, 1896; Backer & Bakhuizen van den Brink, 1963).

SECURIDACA L. Shrubs, lianas, or small trees; 80 species; Africa, South America, and Indo-Malesia. Ovary 1-locular, with 1 epitropous, ventral ovule. Fruit a 1-locular samara with a strongly elongated unilateral wing, up to 7 × 1.5 × 2 cm, pericarp hard (Chodat, 1896).

MOUTABEAE

BARNHARTIA Gleason. Liana; 1 species; South America. Ovary 2- or 3-locular, with 1 epitropous, ventral ovule per locule. Fruit not known (Sprague & Sandwith, 1932).

DICLIDANTHERA Martius. Small trees or lianas; 8 species; South America. Ovary 3- or 5-locular, with 1 epitropous, ventral ovule per locule. Fruit a subglobose, 3- to 5-locular berry, 2.3 × 2.2 × 1.5 cm; mesocarp leathery (Gürke, 1891 (under Styracaceae); pers. obs.).

ERIANDRA Royen & Steenis. Tree to 30 m tall; 1 species; New Guinea and Solomon Islands. Ovary 7- or 8-locular, with 1 epitropous, ventral ovule per locule. Fruit a globose, 7- or 8-locular berry, up to 4 × 4 × 3.5 cm, smooth, first green, ripening orange; mesocarp leathery (Van Royen & Van Steenis, 1952; Van Steenis, 1964).

MOUTABEA Aublet. Trees to 10 m tall, shrubs, or lianas; 10 species; South America. Ovary 4- or 5-locular, with 1 pleurotropous, ventral ovule per locule. Fruit a subglobose, 4- or 5-locular berry, 4.5 × 4.5 × 4 cm, smooth, first dark green, ripening yellow to orange; mesocarp crustaceous, scented, edible (Van Roosmalen, 1985).

XANTHOPHYLLEAE

XANTHOPHYLLUM[2] Roxb. Shrubs or trees 3–50 m high; 93 species; Southeast Asia, Malesia, India, and Australia. Ovary 1-locular, with 4 to 20 epitropous, dorsal ovules. Fruit usually a globose, 1-locular berry, up to 15 × 15 × 15 cm; pericarp usually hard; rarely a subglobose, 1-locular, dehiscent, irregularly 2-valved capsule (Van der Meijden, 1982).

RELATIONSHIPS NOT CLEAR

EMBLINGIA F. Mueller. Shrub; 1 species; Australia. Ovary 3-locular. Fruit not known (Erdtman *et al.*, 1969; Cronquist, 1981).

MATERIALS AND METHODS

Specimens examined are documented in the TABLE. Fixation was with either Allen's modified Bouin's fluid (Johansen, 1940) or a mixture of formaldehyde,

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[2] Although separated by Cronquist (1981), this genus is included in the family by Van der Meijden (1982).

Specimens of Polygalaceae examined.

Species	Collector[1]	Locality	Material[2]	Herbarium[3]
Atroxima afzeliana (Oliver ex Chodat) Stapf	*Bos 6027*	Cameroon	s	WAG
A. liberica Stapf	*De Koning 2903*	Ivory Coast	s	WAG
Bredemeyera densiflora A.W. Bennett	*P.C. Heijligers 2097*	Surinam	fl	U[4]
B. floribunda Willd.	*Balansa 4714*	Paraguay	s	L
B. lucida Klotzsch	*H.L.B. 908.170-67*	Brazil	s	L
B. papuana Steenis	*Kostermans & Soegeng 30*	New Guinea	s	L
	NGF 33220	New Guinea	s	L
Carpolobia alba G. Don	*Breteler 6915*	Gabon	fl/s	WAG
C. gossweileri (Exell) Petit	*J.J. de Wilde 8697*	Cameroon	fl/s	WAG
C. lutea G. Don	*W. de Wilde 512*	Ivory Coast	fl/s	WAG
Comesperma ericinum DC.	*J. Thompson 2927*	Australia	fl	L[4]
C. calymega Labill.	*Ising s.n.* (1968)	Australia	s	L
C. confertum Labill.	*H.L.B. 908.171-761*	Australia	s	L
C. virgatum Labill.	*F. von Müller 5649*	Australia	s	WU
Diclidanthera bolivarensis Pittier	*J.J. Wurdack & J.V. Monachino 41332*	Venezuela	fl	U
	Davidse & Gonzales 1348	Venezuela	s	MO
D. elliptica Miers	*F.C. Hoehne 28421*	Brazil	s	S
Eriandra fragrans Royen & Steenis	*BSIP 1991*	Solomon Islands	s	L
	BSIP 6081	Solomon Islands	s	L
Epirixanthes cylindrica Blume	*Nooteboom & Chai 2318*	Indonesia	s	L
E. elongata Blume	*J.F. Maxwell 76-642*	Thailand	fl/s	L
Monnina ciliolata DC.	*Wendt & Lott 3454*	Mexico	fl/s	L[4]
M. wrightii A. Gray	*Wendt et al. 3457*	Mexico	fl/s	L[4]
	Krapovickas & Schinini 30760	Argentina	s	L[4]
M. xalapensis H.B.K.	*Lott & Wendt P-129*	Mexico	fl/s	L[4]
Moutabea guianensis Aublet	*P.J.M. & H. Maas 2358*	Surinam	fl/s	U
Muraltia heisteria (L.) DC.	*P.H. Roux 6754*	South Africa	s	L
Nylandtia spinosa Dumort.	*Lam & Meeuse s.n.* (1939)	South Africa	s	L
Polygala				
Sect. *Acanthoclados*				
P. klotzschii Chodat	*Hatschenbach 16952*	Brazil	s	L

Sect. *Hebecarpa*				
P. americana A.W. Bennett	*H. von Türckheim 11650*	Guatemala	is	L
P. durandii Chodat	*Antonio Molina R. 18520*	Honduras	s	U
P. jamaicensis Chodat	*K.U. Kramer 1660*	Jamaica	s	U
P. macradenia A. Gray	*C. Wright 1348*	Mexico	is	L
Sect. *Hebeclada*				
P. floribunda Bentham	*Antonio Molina R. & Albertina Molina 27713*	Guatemala	is	U
P. violacea Vahl	*Smith 1309*	Colombia	s	L
Sect. *Ligustrina*				
P. ligustroides St. Hil.	*H.L.B. 908.171-501*	Brazil	s	L
P. membranacea[5] (Miq.) Görts	*G. Stahel 383*	Surinam	s	U
Sect. *Polygala*				
P. conferta A.W. Bennett	*Wendt 3446*	Mexico	fl/s	L[4]
P. microspora Blake	*Maas & Westra 3639*	Surinam	fl/s	U
P. semialata S. Watson	*Wendt 10392*	Mexico	fl/s	L[4]
P. vergrandis W. Lewis	*Johnston, Chiang, & Wendt 12285*	Mexico	fl/s	L[4]
Salomonia oblongifolia L.	*MAK 60355*	Japan	s	MAK
Securidaca atroviolacea Elmer	*P.N.H. 12446*	Philippines	s	L
S. corymbosa Turcz.	*Cuming 1031*	Philippines	s	L
S. diversifolia (L.) Blake	*P. Teunissen s.n.* (1982)	Surinam	fl/s	L[4]
S. ecristata Kassau	*M.S. Clemens 8388*	New Guinea	s	L
S. inappendiculata Hassk.	*Blume 2226 L*	Indonesia	s	L
S. lanceolata A. St. Hil.	*H.L.B. 905.220-60*	Brazil	s	L
S. longepedunculata Fresen	*W.J. de Wilde 10740*	Ethiopia	s	WAG
S. philippinensis Chodat	*P.N.H. 2659*	Philippines	s	L
S. volubilis L.	*H.L.B. 908.171-1340*	Surinam	s	L
S. welwitschii Oliver	*Maas Geesteranus 6309*	Kenya	s	L

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1. If the collector is unknown, the specimen is identified by an institutional number.
2. Abbreviations: is = immature seeds, s = seeds, fl = flowers.
3. Herbarium abbreviations follow those recommended in Holmgren and Keuken (1974).
4. Present as alcohol-preserved material.
5. The position of this species is not clear: it is provisionally classified in *Polygala* Sect. *Ligustrina* (A. Görts-van Rijn, pers. comm.)

propionic acid, and ethyl alcohol. Alcohol-preserved flowers and immature seeds were dehydrated in an ethanol/normal butyl alcohol series, embedded in glycol methacrylate, sectioned at 5 μm with glass knives, stained with periodic acid–Schiff (PAS) reagent (Feder & O'Brien, 1968), and counter-stained with aqueous methylene blue. Ripe seeds obtained from the herbarium were soaked either for three days in a detergent mixture (Alcorn & Ark, 1953) or for two days in 10 percent aqueous ammonia. After imbibition the seeds were directly dehydrated and subsequently infiltrated with glycol methacrylate, without fixation. These seeds gave better results than freshly collected and fixed ones. Hand sections were also made.

For SEM studies alcohol-preserved material was dehydrated with dimethoxymethane (Gersterberger & Leins, 1978), critical point–dried with liquid CO_2, gold/palladium sputter-coated for 3 minutes, and studied on a Cambridge Stereoscan Mark 2A. Phloroglucinol-HCl, Sudan IV, ruthenium red, and iodine in potassium-iodide solution stains were used for specific color tests.

Placentation terminology follows Björnstad (1970) and Radford *et al.* (1974). Descriptions of embryos and endosperm are adapted from Martin (1946) and Smith (1983). In measurements of cells, the radial dimensions are given first, followed by tangential dimensions; descriptions of symmetrical plane figures are done according to Radford *et al.* (1974).

Preliminary research (Verkerke & Bouman, 1980; Verkerke, 1984) has explained the ontogeny of ovules and seeds in *Polygala* and *Xanthophyllum*. For *Comesperma* and *Monnina* ample alcohol-preserved material was available for study of ovules and seeds, and this allowed a description of the complete ontogeny. These results have allowed the ontogeny of incomplete series of other genera to be reconstructed. Many species were only represented by a few (minimum number, 5) seeds obtained from herbarium specimens (see TABLE). To avoid repetition, not all species are equally illustrated: illustrations are intended to show variations in ontogeny leading to differences in seed morphology. Depending on the quality of the material and the purpose of the illustration, a photomicrograph, a scanning electron micrograph, or a camera-lucida drawing has been included. Insofar as possible, stages were described for each specimen in the following sequence: ovule primordium, integument initiation, mature ovule, postfertilization development, and mature seed (inside to outside—embryo, endosperm, nucellar remains, inner integument, outer integument, color, shape, dimensions, indumentum, and appendages).

RESULTS

POLYGALA

SECT. HEBECARPA. In the ripe seed of *Polygala durandii* (FIGURES 1A, 2A), the spatulate embryo has flattened cotyledons measuring 220 × 1700 μm in cross section with an adaxial subepidermal parenchymatic palisade layer. The copious endosperm is up to 175 μm thick and consists of thick-walled cells. Except for the prominent cuticle, nucellar remains are only discernible on the antiraphal side and in the micropylar region. In the outer integument, cells of the inner epidermis have divided periclinally and are slightly elongated. The

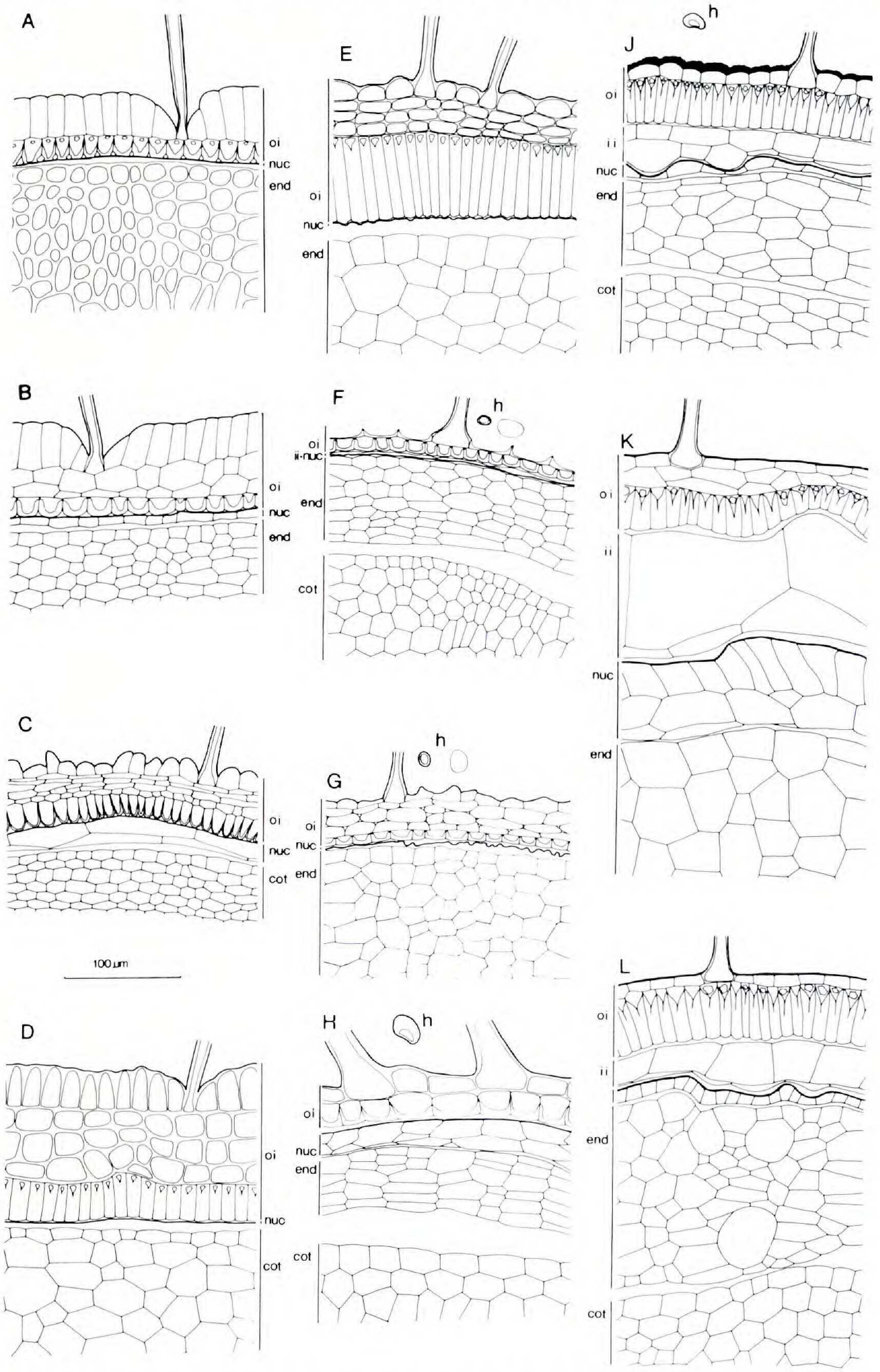

FIGURE 1. Cross sections of polygalaceous seeds: A, *Polygala durandii*; B, *P. jamaicensis*; C, *P. klotzschii*; D, *P. membranacea*; E, *P. violacea*; F, *Bredemeyera lucida*; G, *B. floribunda*; H, *B. papuana*; J, *Comesperma virgatum*; K, *Muraltia heisteria*; L, *Nylandtia spinosa*. (oi = outer integument, ii = inner integument, nuc = nucellus, end = endosperm, cot = cotyledon, h = hair.)

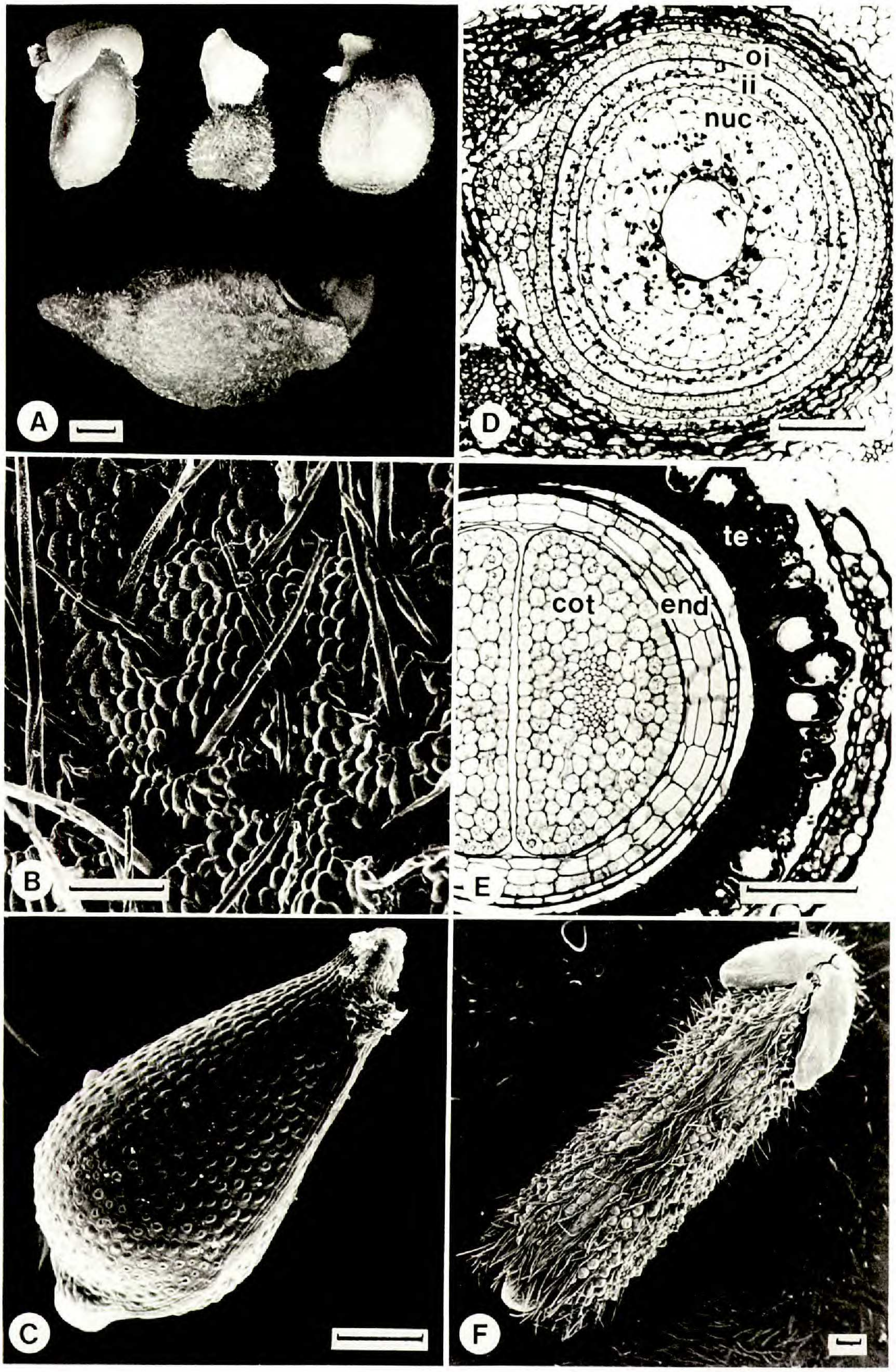

FIGURE 2. Seeds and ovules of species of *Polygala*. A, seeds: top left, *P. jamaicensis*; top center, *P. durandii*; top right, *P. klotzschii*; bottom, *P. membranacea*. B, *P. durandii*, surface of seed. C, *P. microspora*, seed. D–F, *P. vergrandis*: D, mature ovule, cross section; E, mature seed, cross section; F, seed. (Scale bars = 1 mm (A), 100 μm (B, C, E, F), 50 μm (D); symbols as in FIGURE 1.)

short endotesta cells measure 10–12 × 20–22 μm; the distal ends are split along the middle lamella but adhere to the nucellar cuticle. The cell-wall thickening is more pronounced at the distal ends, and frequently the lumina contain a rhombic calcium oxalate crystal. The subdermal mesophyll layer occurs only on the antiraphal side, where it is up to 180 μm thick and consists of globose cells with slightly thickened walls and prominent pits. Since the mesophyll layer is not present on the sides, the seed is strongly laterally flattened. The thin-walled epidermal cells are radially elongated and measure 33 × 13 μm. Some have formed an acicular hair up to 500 μm long with a striate cuticle (FIGURE 2B). The seed is black, slightly flattened, triangular in outline, 5 × 2.8 × 1.2 mm, and has a slightly protruding chalaza. A large, white, bilobed exostome aril extends 2.5 mm over the seed (FIGURE 2A).

In the ripe seed of *Polygala jamaicensis* (FIGURES 1B, 2A), the spatulate embryo has flattened cotyledons measuring 220 × 2500 μm in cross section with an adaxial, subepidermal parenchymatic palisade layer and a thick-walled epidermis. Nucellar remains adhere to the outer integument; the inner integument is crushed. In the outer integument, cells of the inner epidermis are divided anticlinally but are only very slightly radially elongated; the distal portions of the inner epidermal cell walls are thickened. The short endotesta cells measure 10–12 × 15–17 μm. The subdermal mesophyll layer consists of parenchymatic cells and is well developed on the antiraphal side, where it is up to 150 μm thick. On the sides of the seed, it is strongly reduced and only 30 μm thick. The epidermis consists of elongated cells, which have thickened distal walls with a crenulate cuticle. A few cells develop a brown, thick-walled, acicular hair up to 750 μm long. The seed is brown, elliptic in long section and transversely elliptic in cross section, 6 × 2.8 × 1.4 mm, and has a large, yellow exostome aril. The chalaza is located on the ventral side of the base of the seed.

Only immature seeds were available for *Polygala macradenia* and *P. americana*; they were similar to those of *P. durandii*.

SECT. ACANTHOCLADUS. In the ripe seed of *Polygala klotzschii* (FIGURES 1C, 2A), the investing embryo has large cotyledons. The nucellar remains adhere to the endotesta. In the outer integument the cells of the inner epidermis have divided periclinally and are radially elongated. Distally, a weakly developed cell-wall thickening is present and the lumina remain large. The slightly elongated endotesta cells measure 18 × 9 μm. The parenchymatic subdermal mesophyll layer is compressed and up to 15 μm thick. The epidermis consists of irregularly shaped, thin-walled, more or less elongated cells with a cuticle. Some cells have a curled, thick-walled, acicular hair. The seed is light brown, elliptic in long section and transversely elliptic in cross section, 6.3 × 3.3 × 1.5 mm, and has a whitish exostome aril.

SECT. LIGUSTRINA. In the ripe seed of *Polygala membranacea* (FIGURES 1D, 2A), the investing embryo has thick cotyledons measuring 1500 × 3700 μm in cross section. Of the nucellus only the epidermis and the prominent cuticle remain discernible; the inner integument is crushed. In the outer integument the inner epidermis forms an endotesta of elongated palisade cells measuring 30 × 9 μm. The subdermal mesophyll layer consists of thick-walled cells and is up to 60 μm thick. The mesophyll is not restricted to the antiraphal side but occurs throughout the outer integument, as recorded in *P. chamaebuxus* (Verkerke & Bouman, 1980). The epidermis consists of radially elongated cells measuring 30 × 15 μm with thick walls. The seed is brown, orbicular in cross section and elliptic in long section, and 7 × 3.8 × 3.8 mm. The hairy testa has faint ridges running from the apex to the base of the seed, where a firm, pointed chalazal projection 2 mm long is present.

The seed of *Polygala ligustroides* has an investing embryo with thick cotyledons measuring 2000 × 1000 μm in cross section surrounded by a thin layer of endosperm. The nucellus and inner integument are resorbed. In the outer integument, cells of the inner epidermis divide periclinally and are strongly elongated. The palisade cells measure 30 × 15 μm. The subdermal mesophyll layer is up to 50 μm thick. The epidermal cells are not radially elongated and form many unicellular hairs. The seed is black, elliptic in long section and orbicular in cross section, 3 × 2.3 × 2.3 mm. The large, white exostome aril extends over the antiraphal side.

SECT. HEBECLADA. In the ripe seed of *Polygala violacea* (FIGURE 1E), the spatulate embryo has flattened cotyledons measuring 250 × 1300 μm in cross section with a subepidermal palisade layer. The endosperm is copious. The nucellus and inner integument are resorbed, and only the nucellar cuticle remains discernible. In the outer integument, cells of the inner epidermis divide periclinally and are strongly radially elongated. The palisade cells measure 70 × 90 μm. The subdermal mesophyll layer is 40 μm thick; it consists of cells with slightly thickened walls and invests the entire seed. The epidermis consists of slightly thickened, short cells, some with a long, acicular hair. The seed is black, elliptic in long section and orbicular in cross section, 2.7 × 1.7 × 1.7 mm, and has a large trilobed exostome aril; a small chalazal appendage is also present.

In *Polygala floribunda* the immature seed has an endotesta of long palisade cells measuring 50 × 9 μm. The subdermal mesophyll layer is 30 μm thick. In all other seed characters *P. floribunda* is similar to *P. violacea.*

SECT. POLYGALA. The ripe seed of *Polygala microspora* (FIGURE 2C) has a spatulate embryo with plano-convex cotyledons measuring 30 × 80 μm in cross section. The endosperm is copious. In the outer integument an endotesta of strongly elongated palisade cells is formed; the testa does not contain a subdermal mesophyll layer. The epidermal cells are flattened and without hairs. The seed is black, obpyriform in long section and transversely elliptic in cross section, 0.5 × 0.3 × 0.26 mm, and glabrous. Next to the minute white exostome aril is a white raphe and a small chalazal appendage.

In the mature ovule of *Polygala vergrandis,* the nucellus is surrounded by a dermally initiated, 2-layered inner integument. The outer integument is also dermally initiated and completely 2-layered (FIGURE 2D). The subdermal cells on the antiraphal side, seen in *P. vulgaris* (Verkerke & Bouman, 1980), are completely lacking. In the ripe seed (FIGURE 2E) the spatulate embryo has plano-convex cotyledons measuring 150 × 300 μm in cross section. The embryo is surrounded by a thin layer of endosperm, and both are rich in fatty substances. The nucellus is resorbed, with only the epidermis remaining discernible at maturity; the inner integument is compressed. In the outer integument the inner epidermis has a well-developed endotesta of elongated palisade cells measuring 20–50 × 7–10 μm. The mesophyll layer is lacking. Cells of the outer epidermis either have formed acicular hairs up to 300 μm long or are swollen and thin walled, containing numerous PAS-positive inclusions (FIGURE 2E). The small raphe contains an amphicribral strand and is externally characterized by longitudinally enlarged cells; no stomata are present. The seed is black, narrowly elliptic in long section and orbicular in cross section, and 2 × 0.5 × 0.4 mm. It has a white chalazal swelling approximately 100 μm long and a trilobed exostome aril (FIGURE 2F).

Polygala semialata and *P. conferta* differ little from each other in the shape of the seed and aril, but in other seed characters they are similar to *P. vergrandis.*

BREDEMEYERA

In *Bredemeyera densiflora* (FIGURE 3A) the mature ovule is anatropous; the crassinucellate nucellus has a row of 5 parietal cells and a dermal cap 4 cells thick; the embryo sac fills the upper half of the nucellus. The dermally initiated inner integument is 2-layered. In the micropylar region, periclinal divisions in the outer epidermis render the endostome massive. The outer integument is also dermally initiated and 2-layered. A massive exostome develops by repeated periclinal divisions in the inner epidermis. No subdermal cells contribute to the formation of the outer integument (FIGURE 3A). The raphe is 6 or 7 cells thick and contains an amphicribral vascular strand that runs into the unswollen chalazal region, where it branches into a fan of xylem elements. The nucellus-chalaza connection is narrow.

The ripe seed of *Bredemeyera lucida* (FIGURE 1F) contains a spatulate embryo with several collateral strands. The flattened cotyledons measure 240 × 1540 μm in cross section. At the adaxial side of the cotyledon is a subepidermal layer of palisade parenchyma, but a differentiated epidermis is lacking. The embryo is surrounded by a considerable amount of endosperm; both are rich in fatty substances. The nucellar tissue is resorbed, and only the prominent cuticle remains, together with the fully crushed inner integument. In the outer integument the cells of the inner epidermis have divided anticlinally but are only slightly radially elongated; their walls are distally thickened. The lumina are frequently minute and do not contain crystals. The short endotesta cells measure 8–9 × 11–12 μm. The testa lacks a subdermal mesophyll layer. The cells of the outer epidermis are frequently crushed and have thin anticlinal walls. Some cells have long, acicular, thick-walled hairs that are circular in cross section and measure 15 × 15 × 1000–2000 μm. The seed is brown, narrowly elliptic in long section and oblate in cross section, and 7–8 × 1.7 × 1.3 mm. The chalaza, located on the ventral side near the base of the seed, contains vascular tissue and is not swollen. The small raphe is not protruding and contains an amphicribral vascular strand. The thickened, unlobed, hook-shaped, yellow exostome aril is 0.5 mm long; from its apex arises a tuft of thin-walled, white hairs up to 12 mm long and elliptic in cross section. Upon drying, the thick-walled hairs stand erect and the thin-walled ones tend to spread, thus forming an umbrellalike structure.

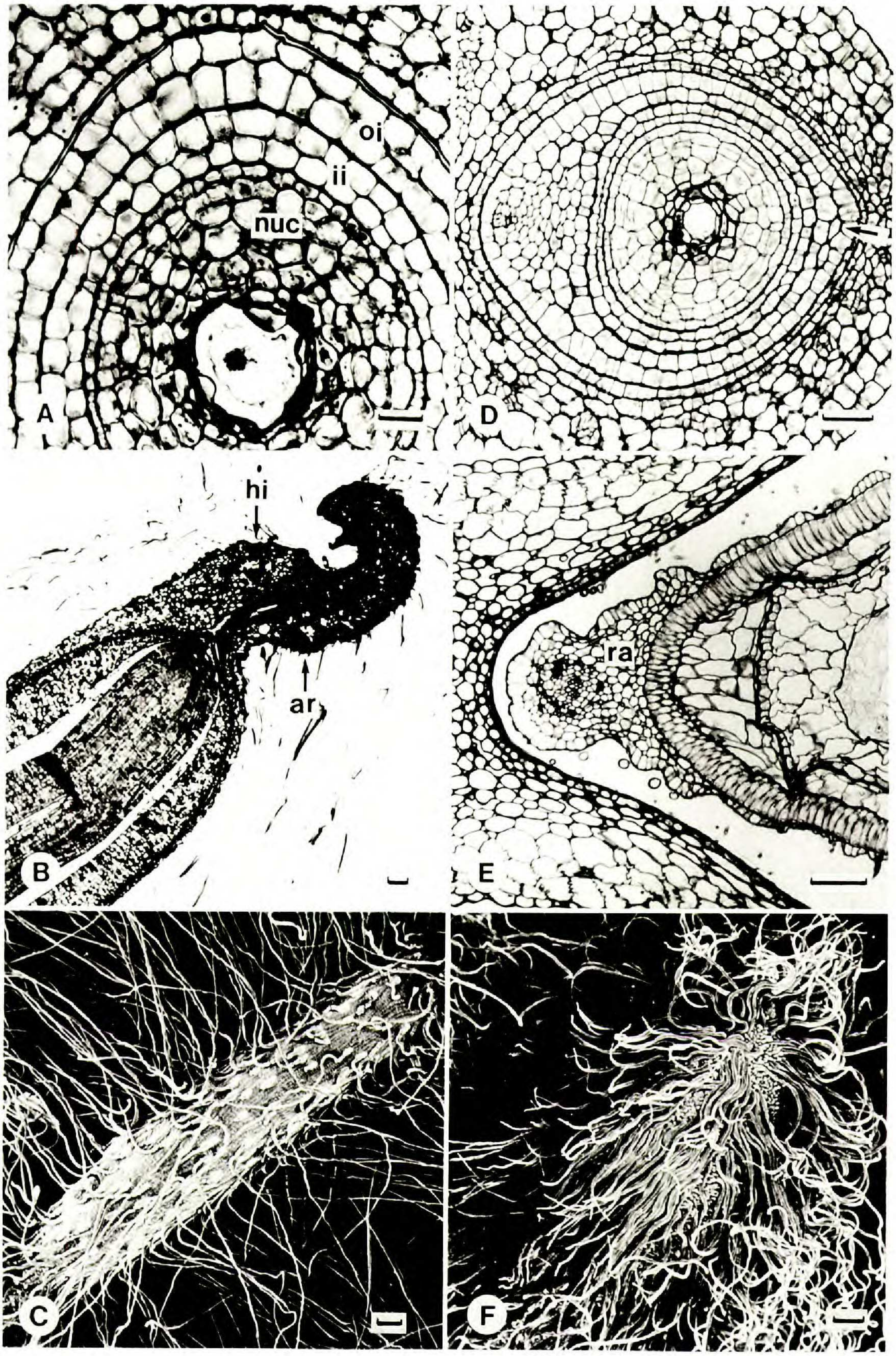

FIGURE 3. Seeds and ovules of species of *Bredemeyera* and *Comesperma*. A, *B. densiflora*, mature ovule, cross section. B, *B. floribunda*, mature seed, long section, micropylar region. C, *B. papuana*, seed. D, E, *C. ericinum*: D, mature ovule, cross section

In *Bredemeyera floribunda* the testa has a subdermal mesophyll layer 10–30 μm thick that consists of parenchymatic, loose tissue with large intercellular spaces. The epidermis consists of irregularly shaped, thin-walled cells (FIGURE 1G). Next to the hook-shaped exostome aril (FIGURE 3B) is a pronounced, vascularized, acicular chalazal appendage measuring 2200 × 500 μm with hairs up to 300 μm long. The seed is brown, narrowly elliptic in long section and orbicular in cross section, and 6.5–7 × 1.1 × 1.1 mm. These characters are in contrast to those of *B. lucida.*

In the ripe seed of *Bredemeyera papuana* (FIGURES 1H, 3C) the embryo is surrounded by a considerable amount of endosperm, the outermost layer of the nucellus, and the partly crushed inner integument. In the 2-layered outer integument the very slightly elongated cells of the inner epidermis measure 19–25 × 25–31 μm and have distally thickened walls. The outer epidermis consists of flattened cells, some of which have developed long hairs with uneven wall thickenings. The raphe is small, not protruding, and contains an amphicribral vascular strand that branches in the chalazal region to form a fan of xylem elements. The ripe seed is brown, narrowly elliptic in long section and transversely elliptic in cross section, and 65–70 × 12 × 10 mm. The chalaza and exostome each have a small appendage.

COMESPERMA

In *Comesperma ericinum* an anatropous ovule with a crassinucellate nucellus develops from a trizonate ovular primordium. The ovule has reduced parietal tissue and a small dermal cap. First the inner integument is initiated in the dermatogen; its primordium is ring shaped. Subsequently, the dermally initiated outer integument appears—on the antiraphal side only, due to the anatropous curvature of the ovule. As soon as the ring of the outer integument has grown to reach the level of the nucellus apically, subdermal cells start dividing and contribute to the outer integument on the antiraphal side.

In the mature ovule (FIGURE 3D) this small subdermal contribution to the outer integument is wedged in between the inner and outer epidermal layers. The embryo sac has extended to fill the upper half of the nucellus; a few parietal cells are still discernible. The inner integument is completely 2-layered. A thickened exostome is formed by repeated periclinal divisions in the inner epidermis of the outer integument. The chalazal region is thickened considerably by periclinal divisions in the subdermal layer, leading to the development of a swelling up to 500 μm long. The nucellus-chalaza connection is very narrow. The raphe is 10 to 12 cells thick and contains a strand of provascular tissue.

After fertilization the ovule enlarges considerably. As soon as the embryo has developed incipient cotyledons, the nuclear endosperm starts resorbing the nucellar tissue. The inner integument is not crushed, and the cells of the outer epidermis enlarge and become radially elongated. In the outer integument, cells

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(arrow indicates subdermal cells in outer integument); E, immature seed, cross section. F, *C. calymega,* seed. (Scale bars = 10 μm (A, D), 100 μm (B, C, E, F); ra = raphe, hi = hilum, ar = aril, other symbols as in FIGURE 1.)

of the inner epidermis divide anticlinally and elongate radially. Subdermal tissue is present as 3 or 4 isolated parenchymatic strands on the antiraphal side. The outer epidermis has divided anticlinally, and some cells have developed long unicellular hairs. The chalaza is distinctly swollen, and the raphe is pronounced (FIGURE 3E); it contains an amphicribral vascular strand that ends in the chalazal region as a fan of xylem elements.

In the ripe seed of *Comesperma virgatum* (FIGURE 1J), the spatulate embryo has plano-convex cotyledons measuring 170 × 500 μm in cross section; they contain provascular strands and lack a differentiated epidermis. The embryo is surrounded by a considerable amount of cellular endosperm; both are rich in fatty substances. Of the nucellus, only the epidermis with the prominent cuticle persists; the inner integument is not crushed. In the outer integument the elongated cells of the inner epidermis form an endotesta of long palisade cells that measure 40–45 × 6–7 μm and have strongly thickened but unlignified walls; the lumina are small, and each contains a rhombic calcium oxalate crystal. The palisade cells are arranged in a regular pattern of domelike structures. The subdermal strands in the testa become completely crushed at maturity. Cells of the outer epidermis lack thickened walls but have a very prominent, finely echinate cuticle up to 4 μm thick. Long, unicellular, white hairs elliptic in cross section and with unevenly thickened walls emerge from the entire surface of the seed. The ripe seed is black, elliptic in long section and oblate in cross section, and 1.5 × 0.9 × 0.7 mm.The seed lacks a large exostome aril but has a minute apical beak and a white chalazal appendage.

In *Comesperma confertum* the entire raphe is white and swollen due to an elongation of the epidermal cells. The seeds of *C. calymega* lack an apical beak. The hairs are straight and appressed to the seed when wet; upon drying they become helically twisted (FIGURE 3F). In all other seed characters *C. confertum* and *C. calymega* are similar to *C. virgatum.*

Previously, Rodrigue (1893) described the endotesta of *Comesperma polygaloides* F. Mueller as having short endotestal cells; no material of this species was available for the present study.

MURALTIA

In the ripe seed of *Muraltia heisteria,* the spatulate embryo has plano-convex cotyledons and is surrounded by copious endosperm. The 2 outer cell layers and the distinct cuticle of the nucellus are persistent. The inner integument persists, and cells of the outer epidermis are greatly enlarged. The inner epidermis of the outer integument constitutes a palisade layer, with cells measuring 20–35 × 15–20 μm (FIGURE 1K). The cells are arranged in a regular pattern of domelike structures, with the inner integument filling the domes. The mesophyll consists of 1 or 2 parenchymatic cell layers. The outer epidermis contains stomata, and a few cells have long, acicular hairs. The raphe contains an amphicribral vascular strand; the mesophyll lacks any post-chalazal vascularization. The seed is brown, elliptic in long section and orbicular in cross section, and 3.8 × 2.6 × 2.5 mm. In the micropylar region there is a white, faintly lobed, 500 × 700 μm exostome aril consisting of parenchymatic tissue.

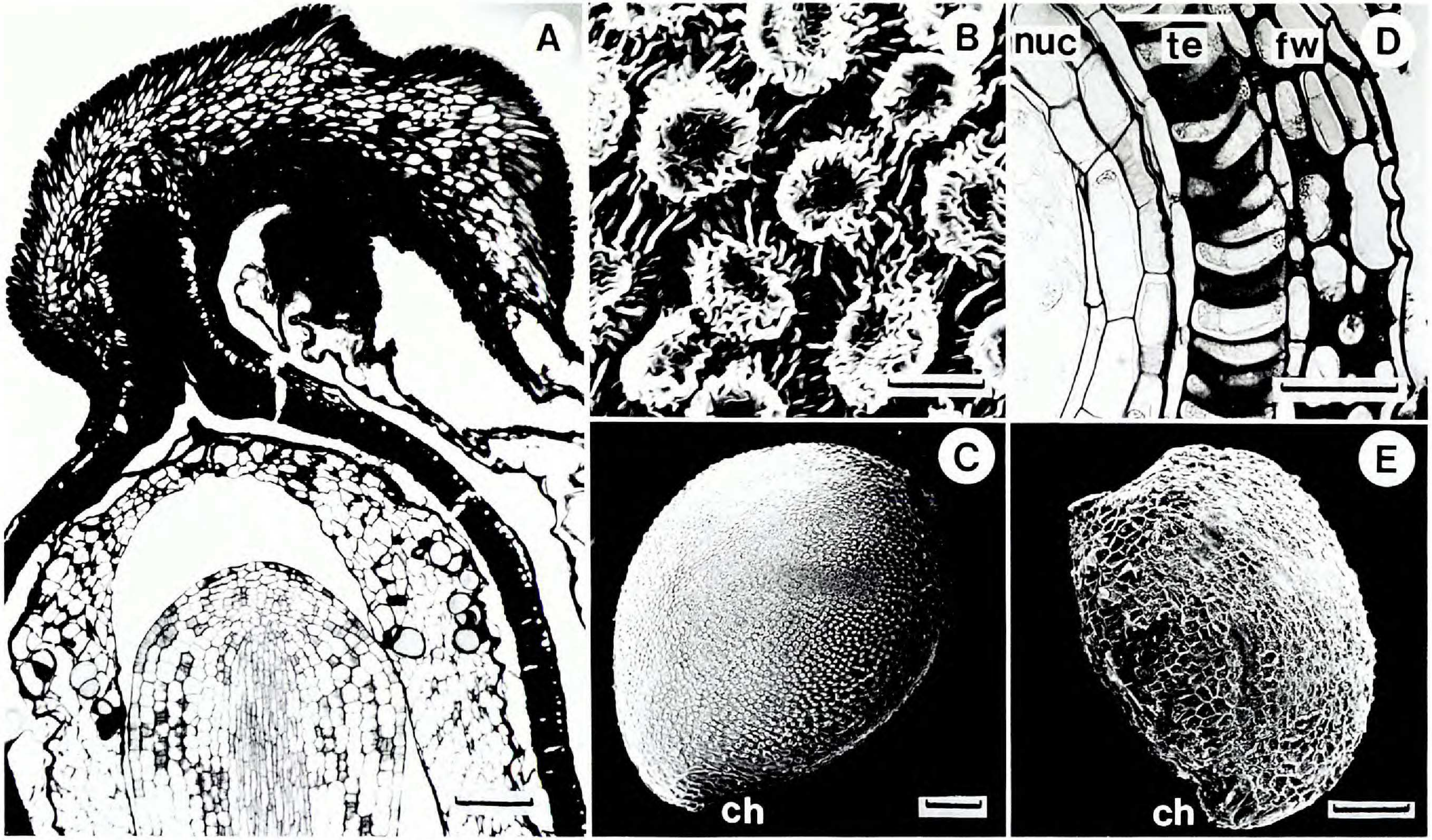

FIGURE 4. Polygalaceous seeds. A, *Nylandtia spinosa,* mature seed, long section. B, C, *Salomonia oblongifolia*: B, surface of seed; C, seed. D, E, *Epirixanthes elongata*: D, immature seed, cross section; E, seed. (Scale bars = 100 μm (A, C, E), 10 μm (B), 50 μm (D); te = testa, fw = fruit wall, ch = chalaza, nuc = nucellus.)

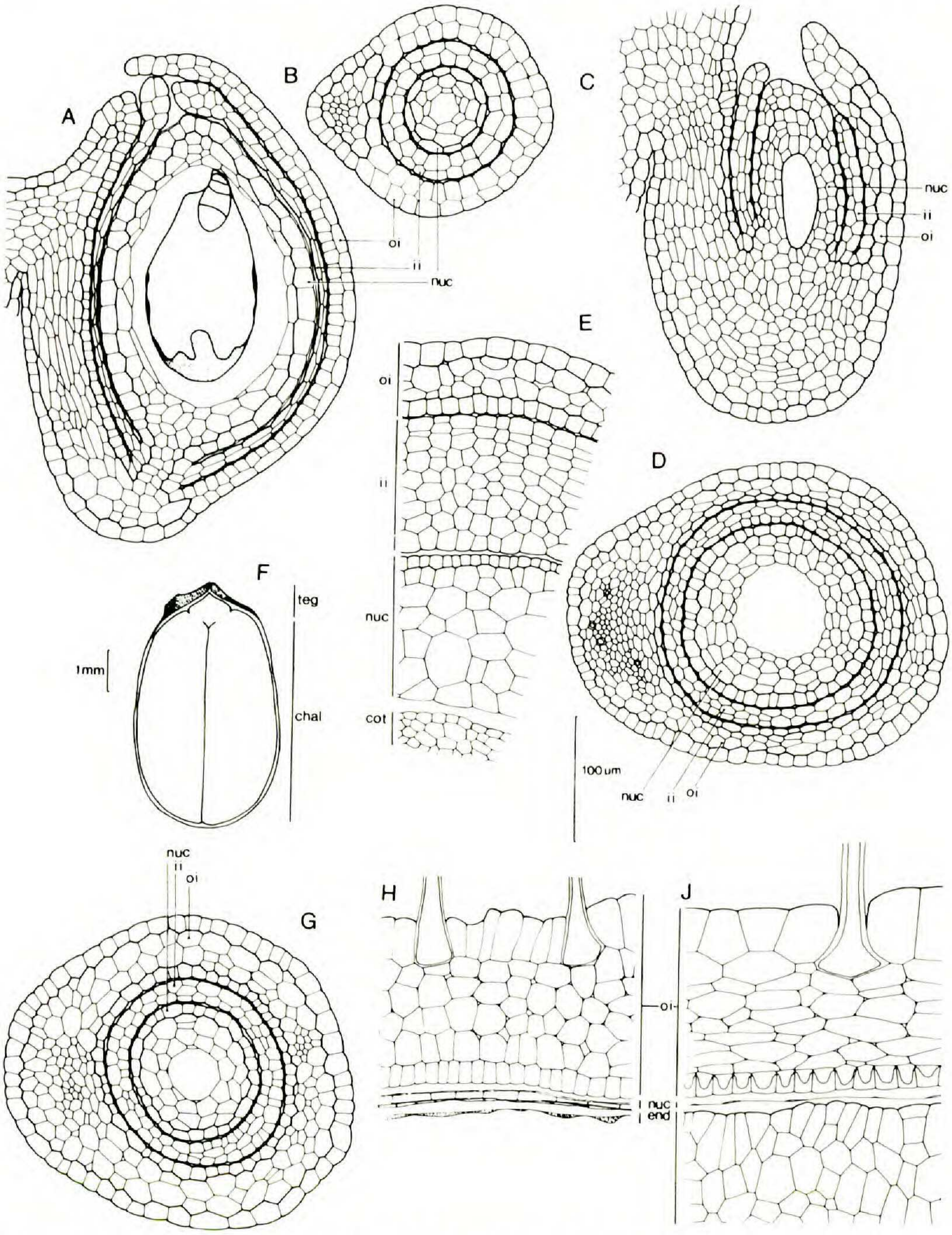

FIGURE 5. Polygalaceous seeds and ovules. A, B, *Epirixanthes elongata*: A, mature ovule after fertilization, long section; B, mature ovule, cross section. C–F, *Securidaca diversifolia*: C, young ovule, long section; D, mature ovule, cross section; E, immature seed, cross section, micropylar region; F, mature seed, long section. G, *Carpolobia gossweileri*, mature ovule, cross section. H, J, *C. lutea*: H, immature seed, cross section; J, mature seed, cross section. (teg = tegumentary part of seed coat, chal = chalazal part of seed coat, other symbols as in FIGURE 1.)

NYLANDTIA

In the ripe seed of *Nylandtia spinosa* (FIGURE 1L), the spatulate embryo has large plano-convex cotyledons 300 × 750 μm in cross section; these contain provascular strands and lack a differentiated epidermis. The copious endosperm contains a few scattered, swollen cells. The nucellus has been resorbed except for the epidermis with a prominent cuticle; the enlarged cells of the outer epidermis of the inner integument are still discernible. In the 2-layered outer integument, the elongated, thick-walled palisade cells of the inner epidermis measure 50 × 8 μm; the reduced lumina contain calcium oxalate crystals. A subdermal mesophyll layer is lacking. The cell walls of the outer epidermis are thin and are sparsely beset with acicular hairs. The seed is brown, widely elliptic in long section and orbicular in cross section, and 5 × 3 × 3 mm. A white exostome aril (FIGURE 4A) with membranaceous lobes extends up to ⅓ the length of the seed.

SALOMONIA

In the ripe seed of *Salomonia oblongifolia,* the plano-convex cotyledons measure 180 × 500 μm in cross section and completely fill the seed; no endosperm is present. The embryo is rich in fat but lacks starch. Except for some thick-walled cells in the micropylar region, the nucellus is resorbed; only the prominent cuticle is still discernible. The inner integument is crushed. The outer integument is 2-layered, and the inner epidermis has formed an endotesta of strongly elongated, thick-walled palisade cells measuring 55–65 × 7–8 μm. The outer epidermis consists of thin-walled, flattened cells that collapse at maturity (FIGURE 4B). The faintly protruding chalaza is not swollen; the raphe has longitudinally elongated cells. The black, exarillate seed is widely obovate in long section and transversely elliptic in cross section, 0.9 × 0.6 × 0.5 mm, and glabrous (FIGURE 4C).

EPIRIXANTHES

The mature ovule of *Epirixanthes elongata* (FIGURE 5A, B) is much smaller than those of the other polygalaceous genera. The crassinucellate nucellus contains reduced parietal tissue and a small dermal cap. The inner and outer integuments are dermally initiated and 2-layered throughout. The raphe is 7 to 9 cells thick and encloses a provascular strand. The small, slightly pointed chalazal region lacks provascular tissue.

After fertilization the ovule enlarges only slightly. The young embryo is initially surrounded by a thin layer of nuclear endosperm, which gradually resorbs the nucellus from the inside outward. The nucellar epidermis develops a prominent cuticle. As the seed ripens, the inner integument is gradually crushed and eventually disappears. In the outer integument, cells of the inner epidermis divide anticlinally and elongate radially (FIGURE 4D). The base of the testa thus becomes 3 cells thick while the distal portion remains 2-layered.

In each of the ripe seeds available for this study, the embryo has incipient cotyledons surrounded by a considerable amount of cellular endosperm, which is rich in fatty substances but contains no starch. Cells of the nucellus top have thickened walls and persist at maturity in the micropylar region of the seed, but the remainder of the nucellus is resorbed except for the epidermis and its prominent cuticle. The endotesta consists of radially elongated, thickened palisade cells with a hexagonal cross section measuring 45–50 × 7–12 μm; the lumina are small and generally contain a calcium oxalate crystal. Cells of the outer epidermis have slightly thickened walls; they do not develop any hairs and are strongly adherent to the endocarp. The white raphal-chalazal swelling strongly contrasts with the testa. The black, exarillate seed (FIGURE 4E) is elliptic with a flattened apex in long section and transversely elliptic in cross section, 0.8 × 0.4 × 0.3 mm, and glabrous.

In *Epirixanthes cylindrica* the outer integument is thickened in the micropylar region by periclinal divisions in the inner epidermis. Ultimately, the testa contains parenchymatic tissue located outside the palisade layer in the micropylar region. The ripe seed is obovate in long section and transversely elliptic in cross section, measuring 0.7 × 0.3 × 0.2 mm. In all other seed characters, *E. cylindrica* is similar to *E. elongata.*

MONNINA

The ovule primordium of *Monnina ciliolata* (FIGURE 6A) has a trizonate structure. The 2 tunica layers, the dermatogen (l_1) and the subdermatogen (l_2), enclose the corpus (l_3). In the subdermatogen the archespore divides into the megaspore mother cell and the parietal cells. In a young ovule (FIGURE 6B) the chalazal megaspore enlarges. The inner integument is dermally initiated, leading to a ring-shaped primordium 2 cells thick.

The outer integument is also dermally initiated and 2 cells thick, but due to the anatropous curvature of the ovule, it appears only on the antiraphal side. When the outer integument is about 10 cells long, subdermal cells start dividing on the antiraphal side (FIGURE 6C) and contribute to its growth. The nucellus has parietal cells and a small dermal cap; the embryo sac has extended, and the oblique orientation of the chalaza-nucellus connection results in the elongation of the integuments on the antiraphal side.

In a mature ovule (FIGURE 6D) the parietal tissue is not resorbed. The micropyle is formed by the inner integument; the top of the outer integument is thickened by periclinal divisions of the inner epidermis. In cross section the subdermal contribution to the outer integument appears as a crescent-shaped group of cells between the inner and outer epidermal layers (FIGURE 7A); in long section the cells are discernible as a subdermal wedge in the proximal part of the outer integument.

The prefertilization development of *Monnina xalapensis* is very similar to that of *M. ciliolata,* but in *M. wrightii* there is no subdermal contribution to the outer integument, so the outer integument is 2-layered throughout.

After fertilization in *Monnina wrightii,* the growing endosperm resorbs the nucellus and the inner integument is crushed. In the outer integument the cells of the inner epidermis elongate radially only slightly. Because anticlinal divisions cannot keep pace with the growth of the ovule, these cells become separated by extensive intercellular spaces (FIGURE 7B, C).

In the ripe seed (FIGURE 7D) the spatulate embryo has flattened cotyledons measuring 300 × 1400 μm in cross section. These lack a differentiated epidermis but have an adaxial, subepidermal layer of palisade parenchyma and

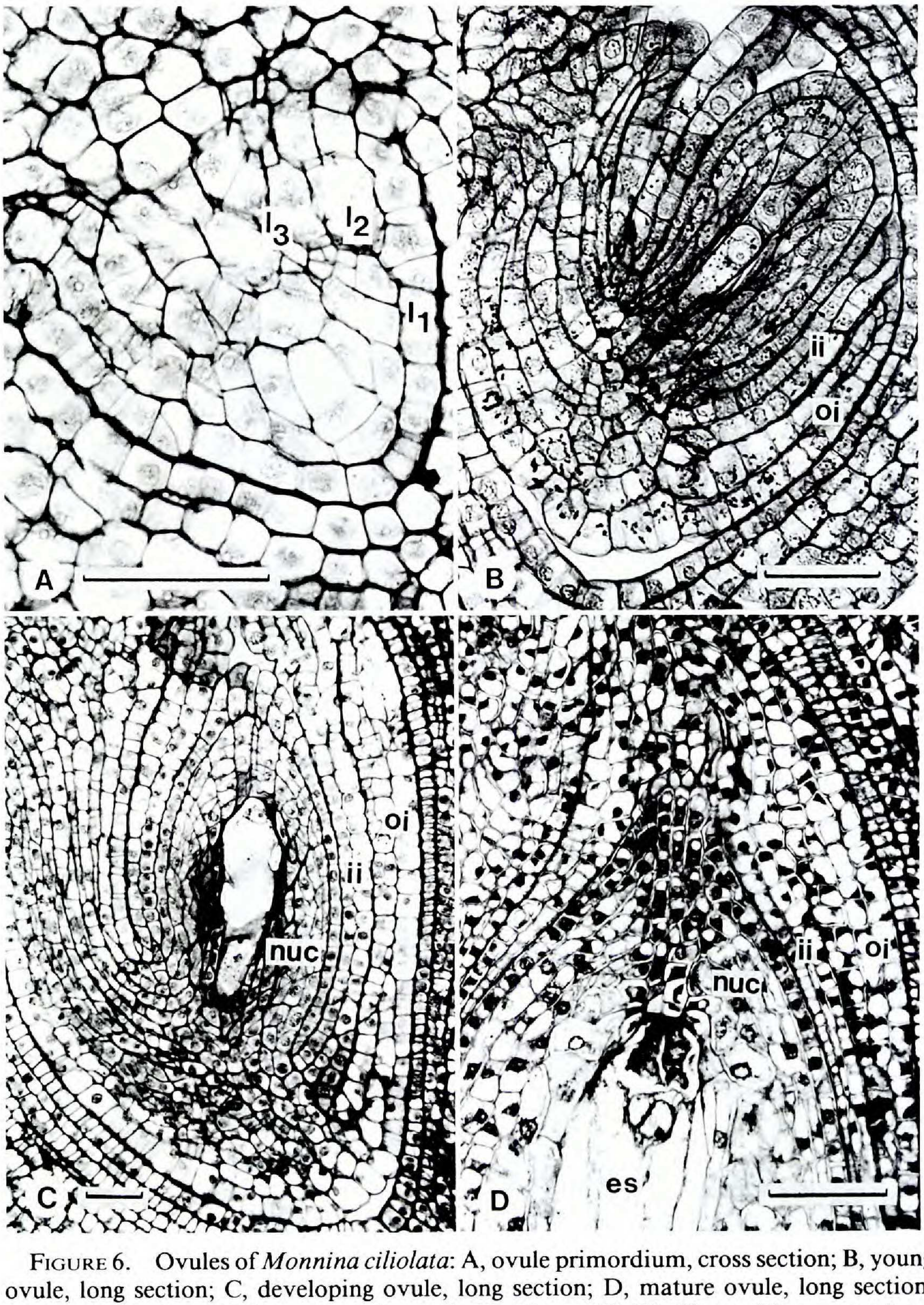

FIGURE 6. Ovules of *Monnina ciliolata*: A, ovule primordium, cross section; B, young ovule, long section; C, developing ovule, long section; D, mature ovule, long section, micropylar region. (Scale bars = 75 μm (A, B), 10 μm (C, D), 50 μm (E); es = embryo sac, l_1 = dermatogen, l_2 = subdermatogen, l_3 = corpus, other symbols as in FIGURE 1.)

well-developed collateral strands. The embryo is surrounded by 3 or 4 cells of endosperm that strongly adhere to the nucellar cuticle. Neither the endosperm nor the embryo contains any starch grains, but both are rich in fatty substances. The inner epidermis of the testa consists of distally thickened cells measuring

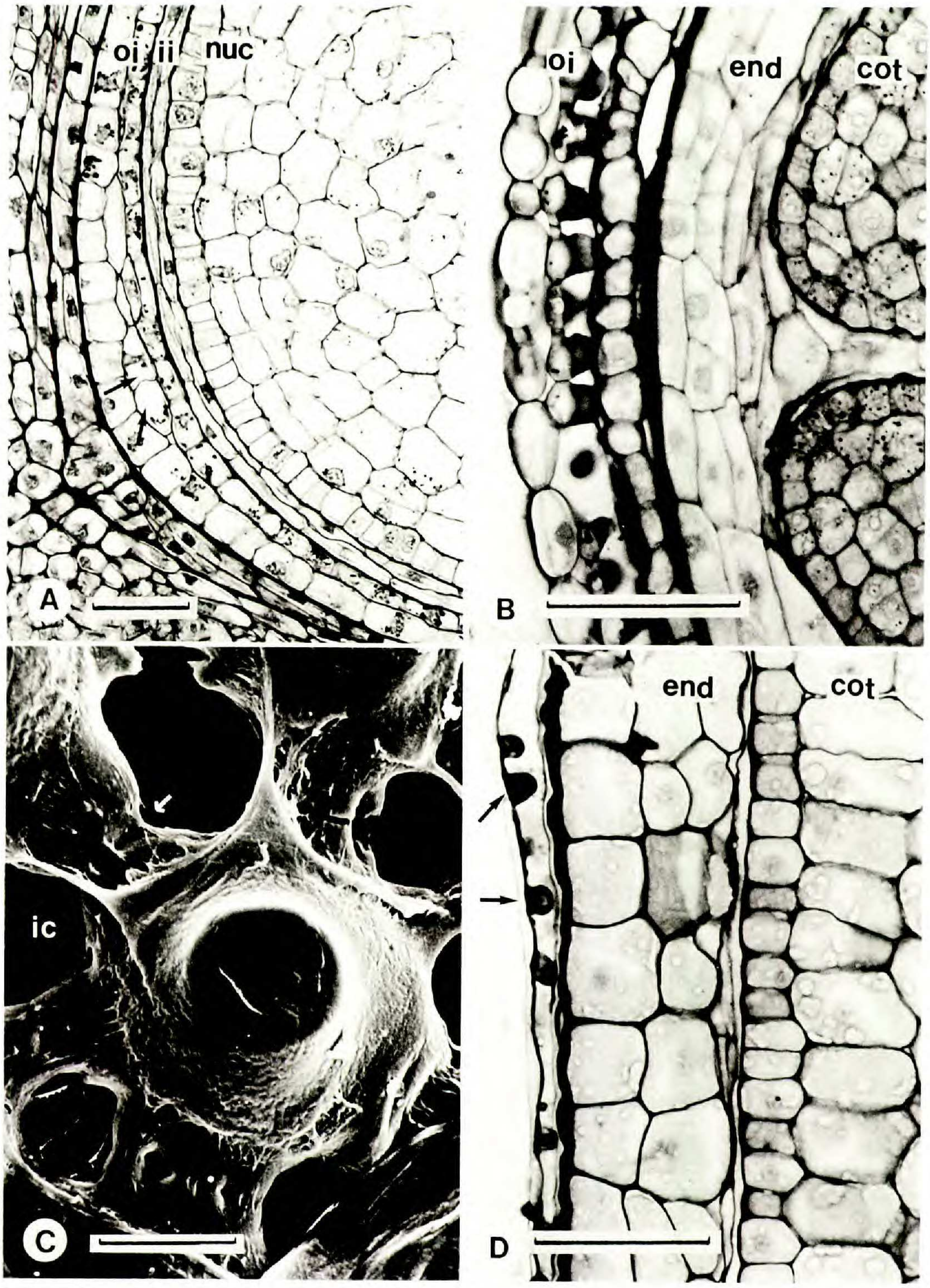

FIGURE 7. Seeds and ovule of 2 species of *Monnina*. A, *M. ciliolata*, mature ovule, cross section (arrows indicate subdermal cells in outer integument). B–D, *M. wrightii*: B, immature seed, cross section; C, reduced testa, interior view (arrow indicates connection between endotesta cells); D, ripe seed, cross section (arrows indicate isolated endotesta cells). (Scale bars = 100 μm (A), 50 μm (B, D), 5 μm (C); ic = intercellular space, other symbols as in FIGURE 1.)

10–11 × 6–7 μm. In growth this is disrupted, and the cells become separated from one another. The cells of the outer epidermis lack hairs and are crushed at maturity. The strongly tanniferous chalazal region, located near the base of the seed on the ventral side, is relatively long and narrow. The raphe contains a small amphicribral vascular strand ending in the chalazal region. The thin, translucent testa follows the form of the embryo. The seed is white, obpyriform in long section, transversely elliptic in cross section, and measures 3 × 1.2 × 0.6 mm. Externally, the isolated, thickened cells of the disrupted inner epidermis are visible as brown dots in the testa; these are more abundant in the micropylar region, where the cells are less separated.

In the ripe seeds of *Monnina ciliolata* and *M. xalapensis,* the inner testal layer is not disrupted and the slightly thickened, light-colored cells still adhere to one another. The seeds are elliptic in long section, transversely elliptic in cross section, and measure 5.5 × 2.3 × 2 mm.

SECURIDACA

Long sections of young gynoecia of *Securidaca diversifolia* show an anatropous ovule with a crassinucellate nucellus (FIGURE 5C), which contains a small embryo sac, a row of 3 parietal cells, and a dermal cap 2 cells thick. The dermally initiated inner integument is 2 or 3 cells thick. The subdermally initiated outer integument is 3 cells thick and has a small, exclusively dermal apex. Periclinal divisions enlarge the chalazal region. The chalaza-nucellus connection is 70 μm wide, and the raphe is 10 cells thick. The cross section of a mature ovule (FIGURE 5D) shows a nucellus with a large embryo sac and an undivided epidermis. The inner integument is 2 or 3 cells thick. The outer integument is 4 or 5 cells thick and consists of an inner epidermis, a mesophyll layer, and an outer epidermis. The mesophyll layer does not contain any provascular tissue. The raphe is 10 to 12 cells thick and contains an amphicribral vascular strand that runs into the thickened chalazal region, branching into a fan of xylem elements.

After fertilization the chalazal region enlarges manyfold, and a pachychalazal development gradually reduces the portion of the seed coat that is formed by the integuments. Initially, the globular embryo is surrounded by a scanty nuclear endosperm, but as the cotyledons develop the endosperm disappears. The nucellus is not yet resorbed, and the inner integument forms a massive endostome by periclinal divisions in the outer epidermis (FIGURE 5E). In the outer integument the cells of the inner epidermis divide anticlinally and elongate radially only very slightly. The mesophyll layer remains parenchymatic, and large intercellular spaces develop (FIGURES 5E, 8A).

In the ripe seed the investing embryo is rich in fatty substances and has large cotyledons 1500 × 3000 μm in cross section. The radicle is located apically, near the micropyle and hilum. The seed is pachychalazal, and the tegumentary part of the testa is restricted to the micropylar region, extending 1.5 mm apically (FIGURE 5F). The vestigial nucellar and inner tegumentary tissues are strongly compressed. In the outer integument the slightly elongated cells of the inner epidermis have faintly thickened walls and contain calcium oxalate crystals

(FIGURE 8A). The mesophyll layer consists of parenchymatic cells with large intercellular spaces; the outer epidermis is not crushed in the tegumentary portion of the testa. The chalazal part of the testa is strongly compressed (FIGURE 8B) and translucent, which makes the extensive and often branching vascularization externally discernible. The ripe seed is yellow and brown in the chalazal portion and dark brown in the tegumentary area; it is elliptic with pointed ends in long section, orbicular in cross section, and measures 6–6.5 × 3 × 2.5 mm.

The ripe seeds of *Securidaca lanceolata, S. ecristata, S. inappendiculata, S. corymbosa, S. atroviolacea, S. philippinensis,* and *S. volubilis* are very similar to those of *S. diversifolia.* The postfertilization development of *S. longepedunculata* and *S. welwitschii* is very different from that of all other species of *Securidaca.*

After fertilization in *Securidaca longepedunculata,* the chalazal region enlarges and shifts toward the dorsal side; no growth occurs in the micropylar region, and as the seed becomes more globose, the micropyle and hilum become located in the middle of the seed on the ventral side. The seed is not pachychalazal, but there is a postfertilization chalazal shift. The investing embryo has thick cotyledons 4 × 9 mm in cross section; the cotyledons contain several collateral strands not confined to the median plane, lack a palisade layer, and have the small radicle located near the micropyle. In the outer integument the elongated cells of the inner epidermis have distally thickened walls (FIGURE 8C). The elongated endotesta cells measure 22–25 × 10–12 μm and are arranged in a regular pattern of domelike structures (FIGURE 8D). The mesophyll and outer epidermis are strongly compressed. The dark brown chalazal region constitutes the dorsal side of the seed; it is elliptic in outline, 3 × 7 mm, and contains vascular tissue but is not tanniferous. The tegumentary portion of the testa is yellow, and the seed is elliptic in long section and orbicular in cross section, measuring 9 × 8 × 8 mm.

CARPOLOBIA

The ovule primordium of *Carpolobia gossweileri* is trizonate and develops into a crassinucellate nucellus with a small amount of parietal tissue. The mature ovule (FIGURES 5G, 8E) has a large nucellus and a small dermal cap; the embryo sac extends toward the chalazal region. The dermally initiated inner integument is 2- or 3-layered and forms an endostome. The subdermally initiated outer integument consists of an inner epidermis, a middle layer of 3 to 5 parenchyma cells, and an outer epidermis. At the level of the nucellus top, the inner epidermis has divided periclinally to form a massive exostome. A small dermal apex is formed on the outer integument. The chalazal region is rather large; the raphe is 11 to 15 cells thick and contains a bundle of provascular tissue that branches in the chalazal region and runs with several small provascular strands into the outer integument.

After fertilization the ovule enlarges manyfold. In *Carpolobia lutea* (FIGURE 5H, J) the nucellus is almost completely resorbed except for fragments of the epidermis and the uninterrupted cuticle; the inner integument is crushed. In

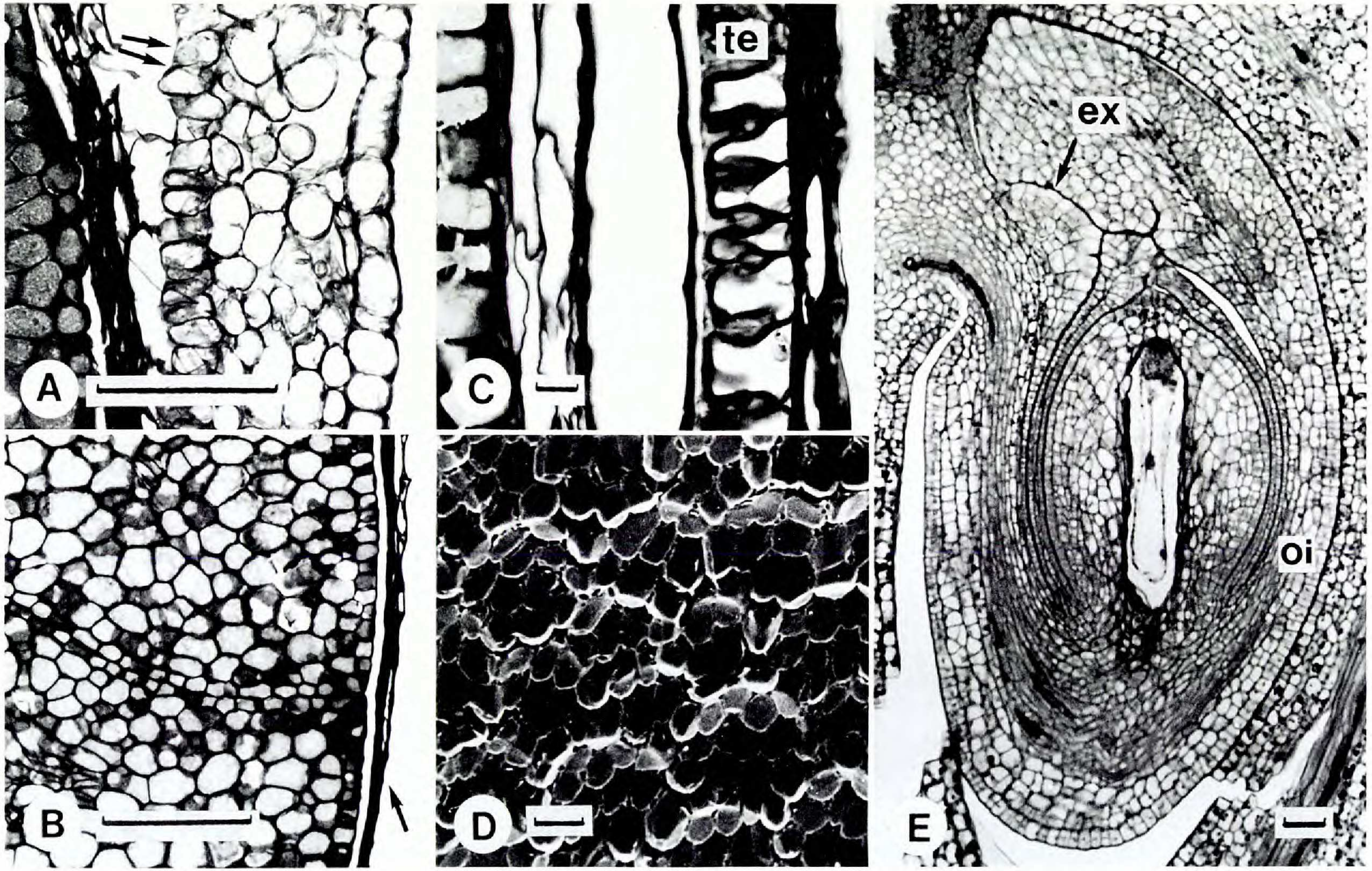

FIGURE 8. Polygalaceous seeds and ovules. A, B, *Securidaca diversifolia*: A, tegumentary part of seed coat, long section (arrows indicate weakly developed endotesta cells); B, chalazal part of seed coat (arrow), long section. C, D, *S. longepedunculata*: C, testa, cross section; D, testa, interior view. E, *Carpolobia gossweileri*, mature ovule, long section. (Scale bars = 75 μm (A, B), 10 μm (C, D), 50 μm (E); te = testa, ex = exostome, oi = outer integument.)

the outer integument, cells of the inner epidermis divide anticlinally and slightly enlarge radially, while those of the mesophyll layer enlarge tangentially and develop intercellular spaces, and those of the outer epidermis either differentiate into moderately elongated cells with thin walls or develop long unicellular hairs with thickened walls (FIGURE 5H).

In the ripe seed the spatulate embryo has a small radicle near the micropyle. The flattened cotyledons measure 130 × 4000 μm in cross section. The endosperm is copious; both embryo and endosperm are rich in fatty substances but poor in starch. Cells of the nucellus and inner integument are still discernible at the chalazal connection, but in the rest of the seed only the nucellar cuticle and compressed vestiges of the inner integument, both strongly adherent to the testa, remain. In the outer integument the cells of the inner epidermis have thickened distal walls, thin proximal walls, and large lumina without crystals; the unlignified short endotestal cells measure 11–13 × 7–8 μm. The mesophyll layer is 60–80 μm thick and consists of faintly thickened, strongly depressed cells. The outer epidermis consists mainly of moderately enlarged thin-walled cells that are rich in fatty substances and measure 50–70 × 40–45 μm; some cells form unicellular, thick-walled hairs up to 2 mm long with a prominent cuticle (FIGURE 5J). The hairs are abundant, especially on the raphe and the antiraphe. The orbicular chalazal region, 800 μm in diameter, is at the base of the seed; it contains vascular tissue but is not tanniferous. The thick amphicribral raphal strand is disrupted in the center; it branches in the chalazal region and runs into the outer integument to form many small strands and a thick antiraphal, amphicribral vascular strand. The long funicle, which shows no traces of aril formation, is near the micropyle at the apex of the seed. The seed is rust colored, elliptic in long section and transversely elliptic in cross section, and 9–11 × 8 × 4 mm.

The examined species of *Carpolobia* vary appreciably in seed-coat structure. In *C. gossweileri* (FIGURE 9A) the endotesta has slightly more elongated cells with less pronounced wall thickenings and thus larger lumina. The distal ends of the short endotesta cells are often slightly split, forming small cavities. The parenchymatic mesophyll is compressed and ca. 20–25 μm thick. As in *C. lutea,* the outer epidermis has differentiated into 2 types of cells, but the thin-walled cells form a layer up to 250 μm thick at the sides and 50 μm at the raphe and antiraphe. The seed is pubescent with many hairs up to 2 mm long; these are particularly abundant on the raphe and antiraphe but also protrude on the sides.

The ripe testa of *Carpolobia alba* (FIGURE 9B) does not form an endotesta. As the seed grows, anticlinal divisions in the inner epidermis do not keep pace with the tangential growth of the mesophyll cells. Eventually, the inner epidermis is disrupted and the compressed inner integument adheres to small, isolated cells on the inside of the testa. Only in the micropylar region is the inner epidermis undisturbed; here it consists of thin-walled, radially enlarged cells. The mesophyll is compressed as in *C. gossweileri,* but the post-chalazal vascularization is restricted to a single antiraphal strand. The outer epidermis has differentiated as in *C. lutea*; the thin-walled cells measure 50–140 × 40–50 μm. The long hairs are sometimes wavy and appressed to the testa. The seed measures 10–12 × 8 × 5 mm—somewhat larger than in the other species.

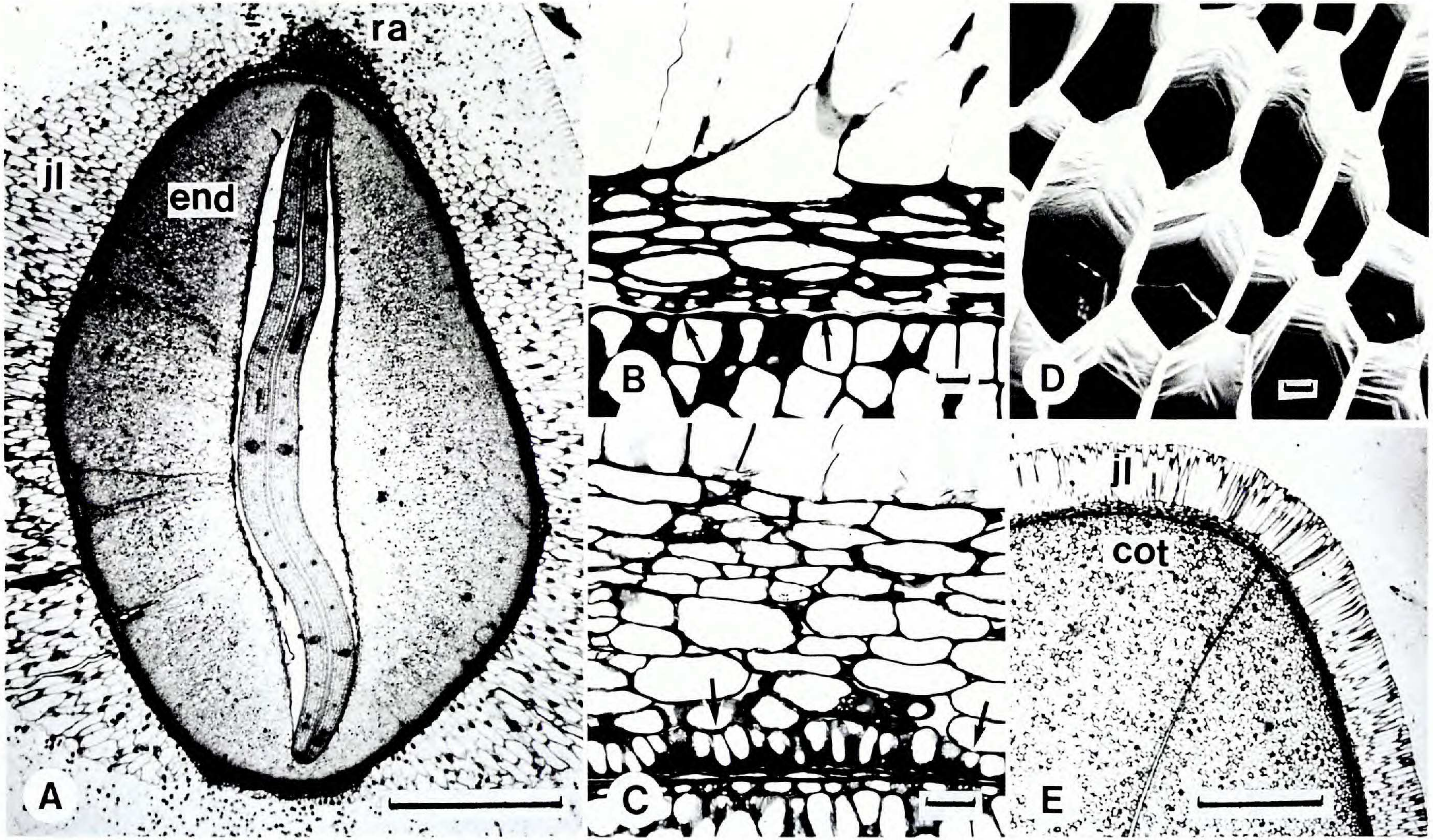

FIGURE 9. Cross sections of polygalaceous seeds. A, *Carpolobia gossweileri,* mature seed. B, *C. alba,* mature testa (arrows indicate isolated endotesta cells). C–E, *Atroxima afzeliana*: C, mature seed coat (arrows indicate endotesta); D, juicy layer; E, mature seed. (Scale bars = 1 mm (A, E), 10 μm (B–D); jl = juicy layer, other symbols as in FIGURES 1 and 3.)

ATROXIMA

In the ripe seed of *Atroxima afzeliana,* the investing embryo has thick cotyledons 7 × 11 mm in cross section. The radicle is near the micropyle and the funicle, on the ventral side near the middle of the seed. Due to a postfertilization shift, the chalazal region constitutes the dorsal side of the seed. The parenchymatic cotyledons have several collateral strands that are not confined to the median plane; the epidermis lacks a cuticle, consisting of depressed cells containing anomocytic stomata. The embryo is rich in fatty substances but poor in starch. A thin layer of endosperm, vestigial nucellar tissue, and inner integument persists in the chalazal region, but in the rest of the seed the embryo is bounded by the outer integument. In the outer integument the inner epidermis has divided anticlinally and has slightly enlarged radially. Distally, the cell walls are slightly thickened and the large lumina lack crystals. The unlignified short endotesta cells measure 12–20 × 10–20 μm (FIGURE 9C). The mesophyll layer is 50–150 μm thick and consists of depressed cells with many intercellular spaces. The outer epidermis has differentiated into a juicy layer (Breteler & Smissaert-Houwing, 1977) consisting of fat-rich, elongated cells with thin walls, measuring 40–45 × 350–550 μm (FIGURE 9D, E). Some epidermal cells, however, have developed a thick-walled, unicellular hair 15 × 15 × 350–550 μm. The chalazal region is strongly enlarged and ellipsoid, measuring 11 × 16 mm; it consists of vascular tissue but is not tanniferous. The testa contains extensive vascularization that emerges from a 3-mm-broad, depressed amphicribral raphal strand that runs into the chalazal region to branch and form many thick post-chalazal strands extending into the mesophyll; no recurrent bundles are present. The micropyle contains a vestigial endostome, and the short funicle shows no traces of aril formation. The seed is brown, reniform with rounded ends in long section and ellipsoid in cross section, measuring 19 × 15 × 9 mm.

The ripe seeds of *Atroxima liberica* differ slightly but characteristically from those of *A. afzeliana.* In the former the inner epidermis of the testa has divided anticlinally, but the cells are depressed instead of slightly elongated and measure 7–8 × 7–13 μm. The mesophyll is 200–500 μm thick, and the elongated epidermal cells are 50–60 × 900–2000 μm. The seed is reniform with tapering pointed ends in long section and almost triangular in cross section, measuring 19 × 15 × 14 mm.

ERIANDRA

The ripe seed of *Eriandra fragrans* (FIGURE 10A) contains a spatulate embryo with a small radicle situated near the funicle on the ventral side. The flattened cotyledons measure 800 × 7000 μm in cross section and contain several collateral strands. The epidermis consists of depressed parenchymatic cells and does not contain any stomata. A considerable amount of endosperm surrounds the embryo; both are rich in fatty substances but poor in starch. The cells of the nucellus are almost completely resorbed by the endosperm but persist in the bulges of the testa. The prominent nucellar cuticle stains deeply in Sudan IV and, together with the compressed remains of the inner integument, strongly

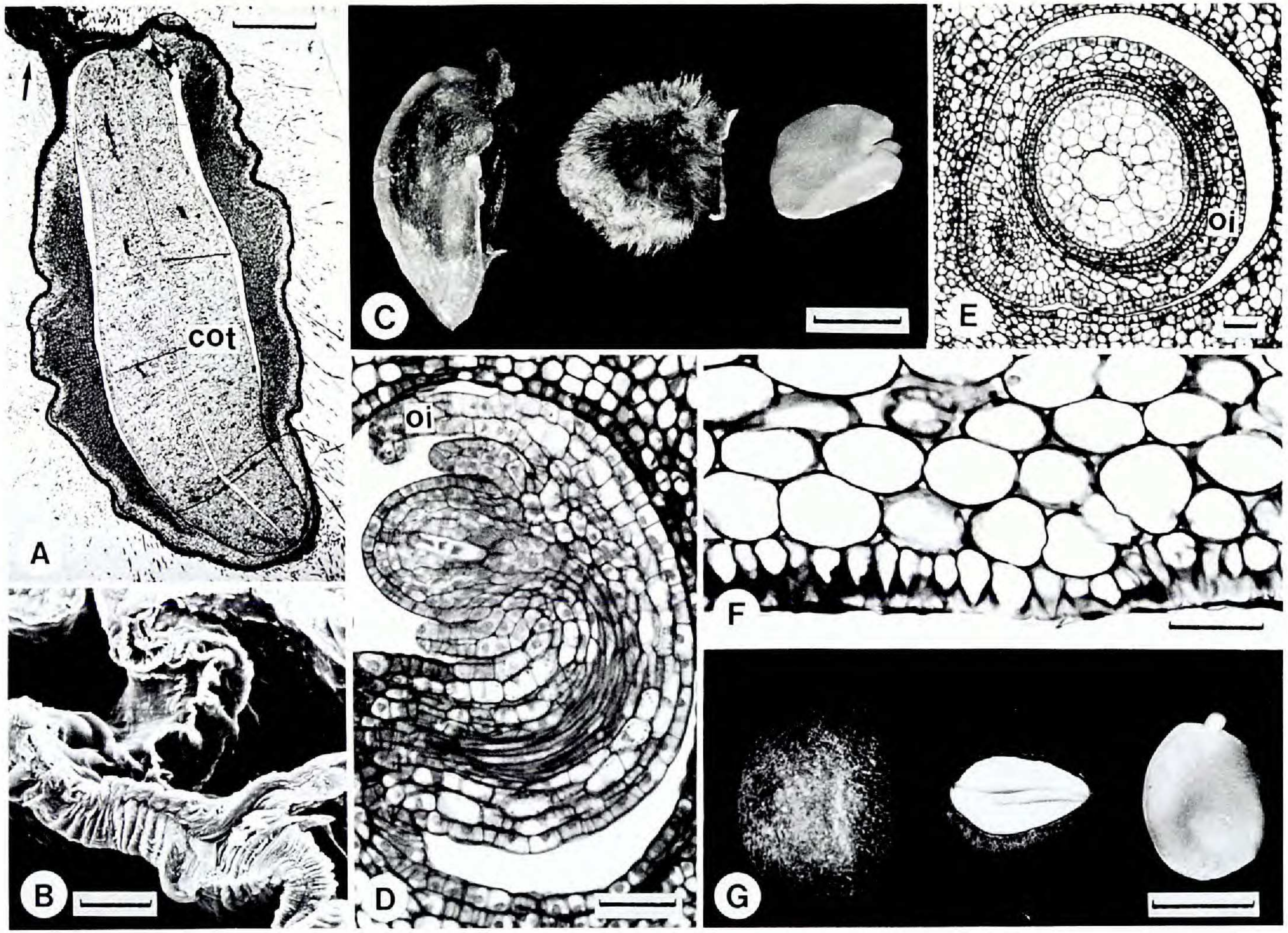

FIGURE 10. Polygalaceous seeds and ovules. A–C, *Eriandra fragrans*: A, mature seed with aril removed, cross section (arrow indicates attachment point of aril); B, scanning electron micrograph of aril, cross section; C, arillate seed (left), seed with aril removed (center), embryo (right). D–F, *Moutabea guianensis*: D, young ovule, long section; E, mature ovule, cross section; F, mature seed coat, endotesta, cross section. G, *Diclidanthera elliptica*: seed (left); seed, cross section (center); embryo (right). (Scale bars = 1 mm (A), 10 μm (B, D, E), 5 mm (C, G), 50 μm (F); symbols as in FIGURE 1.)

adheres to the inside of the testa. In the outer integument (FIGURE 11A), cells of the inner epidermis have divided anticlinally and are only slightly radially elongated; the distal walls of these cells have thickened, while the proximal ones remain thin. The lumina are wide and lack crystals. The endotesta cells measure 25–30 × 16–20 μm and are separated by cavities formed by the splitting apart of neighboring cells along the middle lamella.

The parenchymatic mesophyll layer is strongly compressed, and the relatively thin testa follows the bulges formed by the remains of the endosperm and the nucellus. The outer epidermis forms long, unicellular, rust-colored, slightly thickened hairs that are ellipsoid in cross section and measure 10 × 20 × 1000 μm; both the epidermal cells and the hairs have a prominent cuticle. The hairs are wavy and more or less appressed to the seed coat. The narrow nucellus-chalaza connection is located at the base of the seed; it contains vascular tissue but is not tanniferous. The raphe contains a thick amphicribral vascular strand that runs into the outer integument on the antiraphal side; no recurrent bundles are present. Partly due to additional mesophyll cells, the raphe and antiraphe are externally visible as a pronounced swelling on the seed. The long funicle and the micropyle are in the upper half of the seed on the ventral side. The seed has a large, yellowish, funicular aril that does not follow the bulges of the seed. Viewed in cross section, the aril is up to 400 μm thick and consists of large cells with a finely undulate middle lamella and deeply staining, bulky cytoplasm. The aril is very brittle due to plate collenchyma wall thickenings on the periclinal walls (FIGURES 10B, 11A) (sensitive to ruthenium red); it is completely devoid of fatty substances. The mature seed is brown, widely elliptic in long section and transversely elliptic in cross section (FIGURE 10C), and 8 × 7 × 3 mm.

MOUTABEA

Sections of young gynoecia of *Moutabea guianensis* show anatropous ovules, each with a crassinucellate nucellus and a linear tetrad of four megaspores (FIGURE 10D). The primary parietal cell has divided, and the nucellar epidermis is still 1 cell thick. The inner integument is dermally initiated and 2 cells thick at the apex; it can become 3 cells thick by divisions in the outer layer. The outer integument is subdermally initiated, and its growth is mainly determined by the activity of subdermal cells. Provascular tissue develops in the raphe. The pleurotropous, ventral orientation of the ovule (FIGURE 11B) influences the subsequent development of the ovule and seed.

In the growing ovule (FIGURE 11C) the embryo sac enlarges gradually and nucellar cells divide repeatedly to form a bulky nucellus; the epidermis forms a small dermal cap. The inner integument is generally 2 cells thick. In the outer integument, subdermal activity pushes the dermal portion upward, forming the mesophyll layer that extends to the top of the embryo sac. The inner layer of the dermal apex has divided repeatedly to form thick parenchymatic tissue covering the top of the ovule. The attachment zones of the integuments have shifted away from each other by intercalary growth of nucellar tissue, but the nucellus-chalaza connection is still narrow. Cross sections of a mature ovule

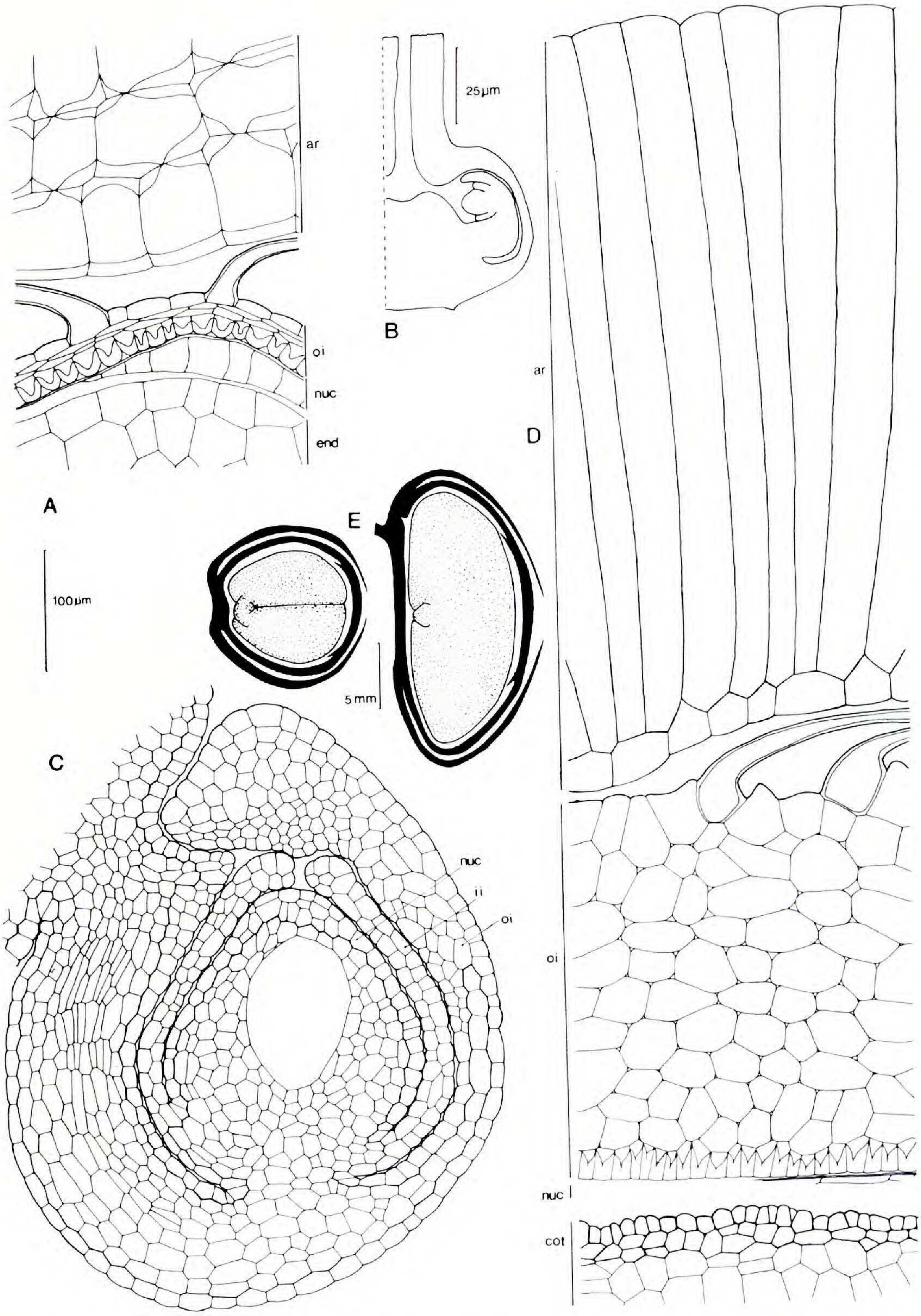

FIGURE 11. Polygalaceous seeds and ovules. A, *Eriandra fragrans,* seed coat, cross section. B–E, *Moutabea guianensis*: B, young gynoecium, long section; C, developing ovule, long section; D, mature seed, cross section; E, mature seed, cross (left) and long (right) sections. (Symbols as in FIGURES 1 and 3.)

(FIGURE 10E) show a large nucellus with an undivided epidermis surrounded by a 2-layered inner integument and a 4- or 5-layered outer integument. The raphe contains an amphicribral vascular strand that branches in the chalazal region and runs into the outer integument.

After fertilization (FIGURES 10F; 11D, E) the ovule enlarges manyfold; the characteristic shape of the seed is mainly due to expansion of the raphal and chalazal regions. The micropyle remains at the top of the seed on the ventral side. At maturity the investing embryo has a small radicle on the ventral side in the middle of the seed. The thick cotyledons measure 4 × 8 mm in cross section and are extensively vascularized by collateral strands. Most of the cotyledonary cells are parenchymatic, but the outer 3 cell layers consist of relatively small cells with thickened walls. The epidermis contains anomocytic stomata and has a cuticle. The dark red embryo is rich in fatty substances but poor in starch.

No stages of endosperm development were available, but the ripe seed does not contain any endosperm. Vestiges of the nucellus and inner integument are discernible at the chalazal connection. In the outer integument the inner epidermis divides anticlinally and the cells elongate slightly in a radial direction to form short endotesta cells measuring 27–30 × 10–12 μm. The cells have proximal walls with little or no thickening, and rather wide lumina without crystals (FIGURES 10F, 11D). The mesophyll layer is 250–300 μm thick and consists of parenchymatic cells with many intercellular spaces. The cells of the outer epidermis are slightly elongated, and some have formed long, curled, thickened, unicellular brown hairs that are ellipsoid in cross section and measure 10 × 20 × 900 μm. Both the hairs and the epidermal cells have a thin cuticle. The attachment zones of the integuments have shifted by intercalary growth, and the endotesta extends beyond the bending point, where a minor space develops; the palisade cells have formed hairs to fill this space. The elliptic chalazal region measures 7 × 12 mm, is not tanniferous, and constitutes the dorsal side of the seed. The raphe contains an amphicribral strand that branches in the chalazal region and vascularizes the rest of the testa; no recurrent bundles are present. The seed is completely surrounded by an unlobed, whitish aril that is attached in the micropylar-raphal area (FIGURE 11E). The aril is 2 or 3 cells thick; the outer cell layer is strongly elongated and 0.05–2.5 mm thick on the dorsal side of the seed, where the ends meet to form a narrow slit. The aril is rich in fatty substances and is adherent to the indumentum. The ripe seed is brown, reniform with tapering ends in long section, orbicular in cross section, and 24 × 13 × 12 mm.

DICLIDANTHERA

The mature ovule of *Diclidanthera bolivarensis* is epitropous and anatropous (FIGURE 12A). The crassinucellate nucellus has a row of 4 parietal cells and a dermal cap 4 cells thick; the embryo sac fills ¾ of the nucellus. The dermally initiated inner integument is 2- or 3-layered (FIGURE 12B). Its outer epidermis forms a massive endostome by periclinal divisions in the micropylar region. The outer integument is subdermally initiated and 5 or 6 cells thick. In the micropylar region repeated periclinal divisions in the inner epidermis of the

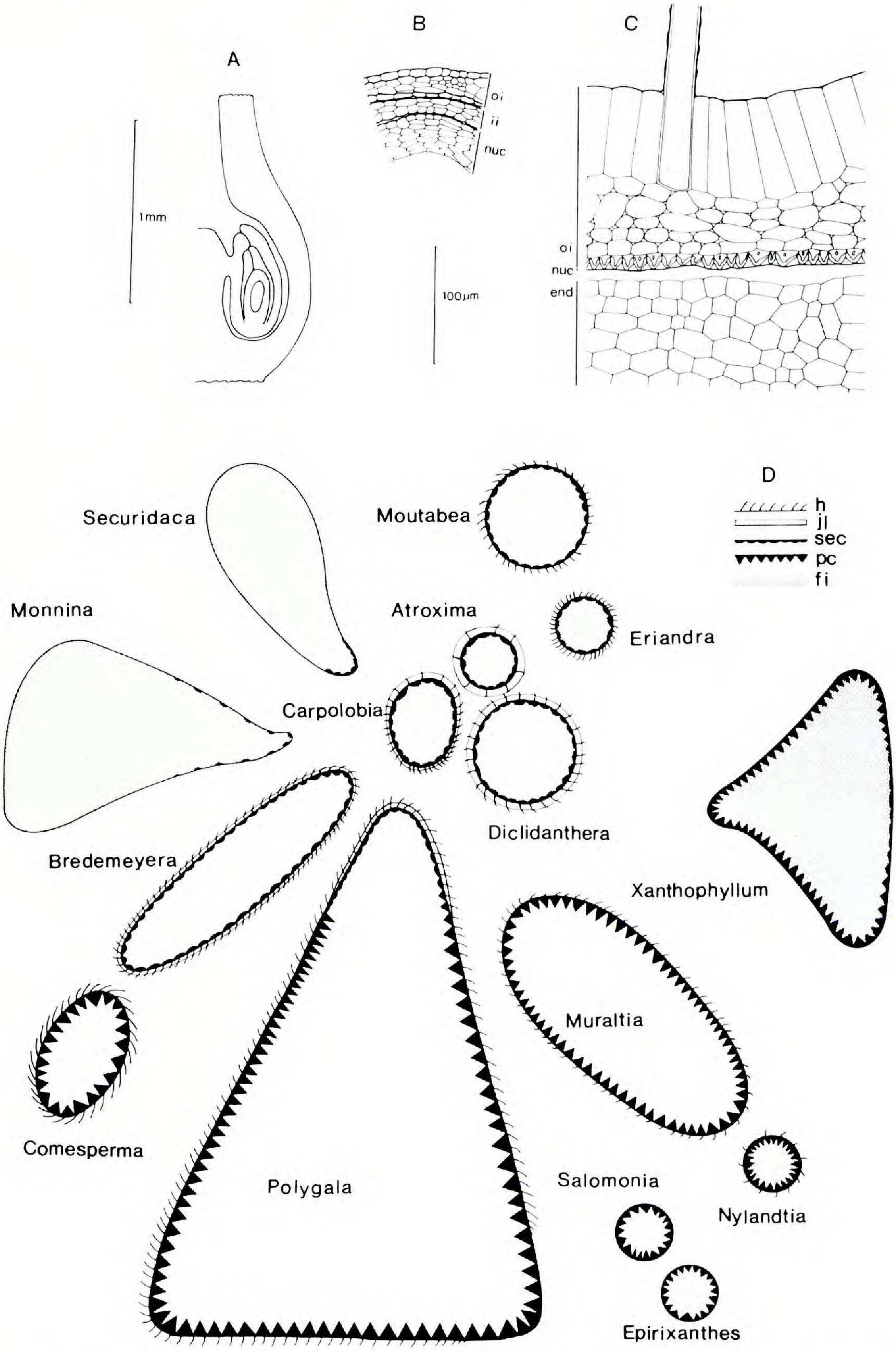

FIGURE 12. A–C, *Diclidanthera bolivarensis*: A, gynoecium, long section; B, mature ovule, cross section; C, mature seed, cross section (symbols as in FIGURE 1). D, imaginary cross section of phylogenetic tree representing taxonomic relationships of polygalaceous genera, based primarily on seed and fruit characters (h = hairy seed epidermis, jl = juicy layer, sec = short endotesta cells, pc = palisade cells, fi = fruit indehiscent).

outer integument render the exostome massive. The raphe is 8 or 9 cells thick and contains an amphicribral vascular strand that branches in the chalazal region and runs together with several small provascular strands into the outer integument.

The ripe seed contains a green, spatulate embryo with a small radicle, situated near the micropyle. The flat cotyledons measure 200 × 6000 μm in cross section. The epidermis consists of small parenchymatic cells and does not contain any stomata; it has a prominent cuticle. A considerable amount of endosperm surrounds the embryo. The cells of the nucellus are completely resorbed; only the prominent cuticle is still discernible. In the outer integument an endotesta is formed by the inner epidermis, the cells of which divide anticlinally but elongate only slightly and measure 9–10 × 10–14 μm. The distal walls are prominently thickened, but the proximal portion of these cells remains thin walled. The cells often have persistent lumina (FIGURE 12C), which frequently contain calcium oxalate crystals. Through splitting of the middle lamellae, a cavity develops between the rounded distal ends of the unlignified short endotesta cells. The mesophyll is 50–70 μm thick and consists of parenchymatic cells with many intercellular spaces. The outer epidermis either differentiates into radially enlarged, thin-walled cells measuring 40–50 × 80–100 μm or develops curled, thick-walled, unicellular hairs up to 400 μm long with a prominent, striate cuticle. The elongated thin-walled cells constitute a juicy layer. The elliptic nucellus-chalaza connection is 300 μm in diameter and is located at the base of the seed. The raphal strand branches in the chalazal region and runs into the outer integument; no recurrent bundles are present. The short funicle and micropyle are apical. The exarillate seed is black, broadly elliptic with a flat base and a more or less pointed apex in long section, transversely elliptic in cross section, and 17 × 7.5 × 5 mm.

The seed of *Diclidanthera elliptica* (FIGURE 10G) has a similar structure and measures 17 × 8 × 6 mm.

DISCUSSION

The Polygalaceae constitute a natural grouping in which small differences in ovule ontogeny are reflected in seed diversity. The ovular primordia are trizonate, and the crassinucellate nucellus has a small dermal cap. At maturity the nucellar tissue is resorbed, and only the prominent cuticle, which frequently adheres to the endotesta, remains detectable. In all genera the two- or three-layered inner integument is dermally initiated. A massive endostome is formed in *Bredemeyera, Securidaca,* and *Diclidanthera.* After fertilization the inner integument is mostly crushed, with just vestiges remaining; only in the ripe seeds of *Comesperma* and *Muraltia* does it persist. The outer integument is subdermally initiated; in the temperate herbaceous genera the subdermal mesophyll layer is gradually reduced. The Polygalaceae represent the first case in which intermediate stages of mesophyll reduction can be shown. Periclinal divisions render the dermal apex of the outer integument massive, and often an exostome aril develops in those genera with bilocular dehiscent fruits. The protective layer of the seed coat is formed by the inner epidermis of the outer integument.

As in the Cruciferae (Vaughan & Whitehouse, 1971), the seed anatomy does not support the current tribal subdivision of the family: the seeds of *Diclidanthera* have more similarities with those of *Carpolobia* than with those of *Moutabea*; seeds of *Securidaca* must be derived from a *Carpolobia*-like ancestor and are not related to *Polygala* seeds. The current tribal subdivisions in the Polygalaceae were already rendered questionable by Styer's (1977) study that indicated similarities in wood anatomy between the Moutabeae, *Bredemeyera,* and *Securidaca.*

In the present study several more or less independently acting evolutionary trends have been recognized that characterize the evolution of the seed. The most important trends are dermalization of the outer integument, decrease in seed size, development of elongated endotestal palisade cells, secondary disruption of the endotesta in some indehiscent fruits, reduction of the juicy layer, chalazal shift, and pachychalazy. Corner's (1976, p. 48) statement that "the main trend in seed-evolution has been simplification by reduction in complexity and size" certainly holds for the Polygalaceae. In her investigation of polygalaceous seed coats, Rodrigue (1893) stated that the testa is reduced when the fruit is indehiscent. The present results show that in the Polygalaceae the situation is not quite that simple: they require the designation of four groups in order to express the interwoven relations of seeds and fruits of the genera adequately (FIGURE 12D).

GROUP 1 (fruits indehiscent, endotesta cells not elongated; *Diclidanthera, Carpolobia, Atroxima, Moutabea, Eriandra*). This group of tropical genera comprises shrubs, treelets, lianas, and a large tree. The berrylike three- to seven-locular fruits contain large seeds with a well-developed seed coat.

The seeds of *Diclidanthera* and *Carpolobia* may represent a prototype from which all other seeds of this and the other three groups can be derived. Both their flattened cotyledons (Eames, 1961; Smith, 1983) and their subdermally initiated outer integuments (Bouman, 1974, 1984) are considered primitive among dicotyledons. The endotesta is not reduced but consists of isodiametric cells with a distal wall thickening. The epitropous placentation is reflected in the orientation of the ripe seed in the fruit. After the seed has ripened, the anatropous ovule simply enlarges into an ellipsoid, flattened seed with an apical micropyle and a basal chalaza; the radicle is directed upward. The epidermal cells differentiate into two types—more or less elongated, thin-walled cells, or polygalaceous hairs. In *Carpolobia* the thin-walled cells are only slightly elongated and the hairs are long and wavy. In *Diclidanthera* the thin-walled cells are relatively more elongated and constitute a juicy layer; the hairs are long and curled. The differences in seed indumentum between *Carpolobia* and *Atroxima* are gradual: in the latter the juicy layer is more strongly developed and the pubescence is sparser. The packing of the large embryo in *Atroxima* requires a specialized seed structure different from that of the preceding genera. After fertilization no growth occurs in the micropylar region, but the chalaza shifts toward the dorsal side, and at maturity the enlarged chalaza constitutes the dorsal side of the reniform seed. The micropyle and the hilum are located in the middle of the seed on the ventral side, and the radicle is oriented toward the floral axis. The chalazal shift is caused by growth more pronounced in the raphe than in the antiraphe, as in the obcampylotropous seeds of some Leguminosae (Corner, 1976). The chalazal shift allows better vascularization of large seeds and expansion of the seed above the funicular attachment. The differences in cotyledon anatomy between *Carpolobia* and *Atroxima* correspond with a different germination type: epigeal in *Carpolobia,* hypogeal in *Atroxima* (Breteler & Smissaert-Houwing, 1977). The present results confirm the conclusions of Breteler & Smissaert-Houwing (1977), who regarded the rambling *Atroxima* as derived from the closely related treelet *Carpolobia.*

The fruits of *Diclidanthera, Carpolobia,* and *Atroxima* are brightly colored, exposed, and large. The mesocarp is often fleshy (*Carpolobia*); the endocarp contains no hard structures and is sometimes glossy inside (*Atroxima*). The exarillate seeds contain a fat-rich juicy layer of elongated epidermal cells (as in *Punica granatum*) that is mixed with polygalaceous hairs. This suggests a dual function of the epidermis—both attracting and repelling animals.

These seed and fruit characteristics fit in well with Van der Pijl's (1982) syndrome of ornithochorous diaspores. Whether birds are attracted by the colored fruits and by the oily juicy layer needs investigation, but it is tempting to speculate that some frugivorous animals open the fruit, suck the seed, and throw it away because of the polygalaceous hairs. Zoochory explains why the endotesta has not been eliminated in the seeds in this group, as it has in the seeds of most of Group 4. Apparently the protective function of the testa has not been taken over by the endocarp, and the fruit and seed operate as a finely regulated dispersal unit.

The seeds of *Moutabea* are considered to be highly specialized because of the more strongly developed endotesta, the orientation of the large embryo, and the thick cotyledons with a thick-walled outer layer and stomata. At the outset the aberrant, pleurotropous ventral placentation orients the ovule so that the chalaza is dorsal (FIGURE 11B)—an evolutionary shortcut toward a chalazal shift. The aril covers the micropyle after fertilization and is attached over the entire ventral side of the seed; it consists of fat-rich parenchymatous cells and is strongly adherent to the seed hairs. The juicy layer of epidermal cells is lacking.

Field work by Van Roosmalen (1985) in Surinam indicates that fruits of *Moutabea guianensis* are distributed by monkeys of the genus *Ateles.* After the red exocarp deteriorates, it contrasts more with the yellowish, scented mesocarp and monkeys are attracted. They crack the fruits and suck the aril; the curled, firm hairs prevent them from chewing. Other monkey species are also attracted, but they chew the seeds, which subsequently fail to germinate. The seed hairs provide the main protection, but the strongly developed endotesta might also be a factor. The fruits and seeds of *Moutabea* are well adapted to monkey dispersal, which is generally considered to be derived: monkeys are relative late-comers in evolution, and they frequently open externally hard fruits with internal soft arils (*Garcinia* sp.; *Mammea* sp.) more easily than birds can (Van der Pijl, 1982).

In *Eriandra* the endotesta is similar to that of *Diclidanthera,* but the seed is not as primitive. The mesophyll layer in the seed is compressed, and the epidermis has developed wavy hairs, but the juicy layer is lacking. The embryo is intermediate between those of *Diclidanthera* and *Moutabea* with regard to size and orientation. Any animal-plant connection is less clear than in *Moutabea*; the funicular aril is devoid of fatty substances, and the peculiar wall thickenings suggest some function involved in the fruit dehiscence at germination. Monkeys are precluded because they do not occur in New Guinea or the Solomon Islands. The derived status of *Eriandra* is also indicated by Styer (1977), who showed that the wood of this large tree has many advanced characteristics of lianas.

GROUP 2 (fruits dehiscent, endotesta cells not elongated; *Polygala* sects. *Hebecarpa* and *Acanthocladus*; *Bredemeyera*). This group comprises tropical South American taxa, mainly shrubs and some lianas. Fruits and seeds are much smaller than those of the taxa in Group 1. The fruits are often fleshy, bilocular dehiscent capsules with arillate seeds. The cotyledons are flat and contain palisade parenchyma. The endotestal cells are not elongated and are frequently split along the middle lamellae, as in *Eriandra* and *Diclidanthera.* In cross section the subdermal mesophyll layer is uninterrupted in *Bredemeyera floribunda* and *Polygala* sect. *Acanthocladus,* laterally strongly reduced in *Polygala* sect. *Hebecarpa,* and not discernible in the ripe seeds of *Bredemeyera lucida.* The reduction of the mesophyll represents a dermalization of the outer integument, as recorded in *Polygala vulgaris* (Verkerke & Bouman, 1980). The epidermis in *Polygala* sect. *Hebecarpa* is very similar to that of *Diclidanthera,* involving a juicy layer mixed with hairs. The thin-walled, irregularly shaped epidermal cells occurring in *Polygala* sect. *Acanthocladus* and in *Bredemeyera floribunda* are also present in *B. collettioides* (Philippi) Chodat and *B. microphylla* Hieron. (Rodrigue, 1893) and are interpreted as remnants of the juicy layer. The seeds have an exostome aril that is yellowish in *Polygala jamaicensis* and *Bredemeyera* but white in the other species of *Polygala*; it is usually trilobed and glabrous. Only in *Bredemeyera* is it hook shaped and does it have a coma of long hairs. In Group 2 the fruits are often fleshy, and the dehiscence seems not so well organized as in the sutured, often marginate, membranaceous capsules of the species of *Polygala* in Group 3 (pers. obs.).

I have concluded that both seeds and fruits of Group 2 are intermediate between those of a *Diclidanthera*-like predecessor and those of Group 3. Obviously, the seeds of Group 2 are not primitive, and with regard to a *Diclidanthera*-like predecessor they show some clearly new acquisitions—for example, the palisade parenchyma in the cotyledon, the thick-walled endosperm in *Polygala durandii,* and the strong reduction of the mesophyll in *Polygala* sect. *Hebecarpa.* The newly developed exostome aril is correlated with fruit dehiscence.

Within *Bredemeyera* much variation in the chalazal appendages and the subdermal mesophyll layer exists, but seed anatomy indicates a close relationship between *Bredemeyera* and *Polygala* sect. *Hebecarpa.* In *Polygala* sect. *Acanthocladus* the *Diclidanthera*-like endotesta cells are slightly more elongated, the subdermal mesophyll is not reduced, and the cotyledons are thick. This suggests a divergent evolution of *Polygala* sects. *Hebecarpa* and *Acanthocladus.*

GROUP 3 (fruits dehiscent, endotesta cells much elongated; *Polygala* pro parte, *Comesperma, Muraltia, Nylandtia, Salomonia, Epirixanthes*). This group comprises shrubs and perennial and annual herbs of tropical and temperate regions. Generally the fruits are membranaceous bilocular capsules containing small, arillate seeds with a genuine palisade layer; the mesophyll layer is frequently reduced.

The endotesta consists of strongly elongated palisade cells that contain calcium oxalate crystals and are frequently arranged in a regular pattern of domelike structures. The reduction of the subdermal tissue in the outer integument (integument dermalization), first recorded in *Polygala vulgaris* (Verkerke & Bouman, 1980), contributes to the neotenic decrease in seed size; it is widespread in the seeds of Groups 2 and 3, which are borne in a bilocular capsule. The mesophyll is well developed in *Polygala* sects. *Hebeclada, Ligustrina,* and *Chamaebuxus,* and in *Muraltia.* The lateral reduction of the mesophyll flattens the ovule (Verkerke & Bouman, 1980, *figs. 11, 12*), and a further reduction to smaller seeds leaves only a small strand of subdermal tissue wedged in between the inner and outer epidermal layers on the antiraphal side. In the herbaceous *Polygala* sect. *Polygala* one (and in *Comesperma* three or four) antiraphal mesophyll strands are present. Ultimately, fully dermal testae develop in the smallest seeds. The testae of *P. vergrandis, P. microspora, P. conferta, P. semialata, Salomonia, Epirixanthes,* and *Nylandtia* are fully dermal; in the latter genus Rodrigue (1893) apparently confused testa and endocarp.

The epidermis usually has unicellular, erect and silky (many species of *Polygala; Muraltia, Nylandtia*) or extremely elongated (*Comesperma*) hairs. In the smallest seeds (*P. microspora, Salomonia, Epirixanthes*) the hairs are lost altogether, and some epidermal cells form only a small papilla (FIGURE 2C). Only in *P. membranacea* do the radially elongated, thick-walled cells resemble the epidermal juicy layer in the seeds of Groups 1 and 2.

In most *Polygala* species, *Nylandtia,* and *Muraltia,* the white exostome aril is trilobed. The extreme variation of the aril in *Polygala* baffled Chodat (1890–1893), who did not then know about the myrmecochory of the seeds first reported by Sernander (1906). Myrmecochory has been established in several European and Australian *Polygala* species and in *Comesperma* species (Berg, 1975) but may have been largely overlooked in other regions (Beattie, 1983).

The raphe and chalaza can be swollen (FIGURE 2F), as well as the exostome. In *Comesperma* the exostome aril is reduced, and the white chalazal and raphal swellings have become ant attracting. The small seeds of *Polygala microspora* have only minute seed appendages. The large, thin-walled capsule is distinctly swollen, which suggests possible fruit transport through the air. In *Salomonia* the exarillate seeds are borne in a spiny capsule; this suggests epizoochory. Epizoochory was also recorded in *P. glochidiata* (Huth, 1887), but unfortunately this has never been confirmed.

In Group 3 plano-convex cotyledons are without palisade parenchyma and are surrounded by an often copious endosperm. This occurs in many *Polygala* species and in *Comesperma, Muraltia,* and *Nylandtia.* The exalbuminous seeds of *Polygala* sect. *Ligustrina* and, according to Corner (1976), also those of *P. venenosa* subsp. *pulchra* contain thick, fleshy cotyledons. The variation in cotyledon anatomy between genera and infrageneric groups presented here obviously hinders a simple characterization of the family but also reflects the divergent evolution of the taxa concerned.

Bresinsky (1963) noted that elaiosomes (as present in *Polygala*) are frequently separated from the seed by thick-walled structures that force ants to consume only the elaiosome and to reject the seed proper. Van der Pijl (1982) notes that a palisade layer renders seeds more fit for life outside the rain forest. The similarities between the seeds of Groups 1 and 2 indicate that initially fruit dehiscence did not force many internal changes in the smaller, arillate seeds of Group 2. The development of a palisade layer and a narrow nucellus-chalaza connection in Group 3 both prevented undesirable predation by the newly attracted dispersers and served as a better protection against desiccation, thereby allowing the colonization of new habitats outside the rain forest. This was accompanied by a changeover from flat cotyledons with palisade parenchyma to plano-convex ones.

In *Polygala* the tendency toward a herbaceous habit is accompanied by a decrease in seed size, but this mainly results in a flattening of the seed. Dispersal by ants is frequently coupled with a special myrmecochorous syndrome (Berg, 1975) that might also lead to anemochory of fruits. Ulbrich (1928) described the diplochorous dispersal of *Polygala vulgaris* and noted that ripe fruits, which are membranaceous, laterally flattened, and marginate, are blown off the plant by the wind. Once the fruit has fallen on the ground, a locule opens and exposes the seed (pers. obs.). Seed flattening in *Polygala* might indirectly flatten the capsule, which may have led to the diplochorous form of dispersal.

The seeds of *Polygala venenosa* subsp. *pulchra* (Corner, 1976) are not necessarily ancestral to the derived representatives of the genus. In addition to the thick cotyledons, it has some derived characters that suit the seed to the reported endozoochorous bird dispersal (Ridley, 1930). The palisade cells are extremely elongated (up to 240 μm), and a large red aril partly covers the globose, black, glabrous seed; the persistent capsule valves add further to the bird-attracting color contrast (see Van Steenis, 1972). The aril is basically of the same construction as the smaller, white, ant-attracting caruncle of the herbaceous species of *Polygala.*

The genus pairs *Muraltia-Nylandtia* and *Salomonia-Epirixanthes* show many similarities in seed structure with *Polygala. Muraltia* resembles the more primitive species of *Polygala* in having an uninterrupted mesophyll layer and an exostome aril. *Nylandtia* differs in the reduction of the mesophyll layer, but the secondary closure of the fruit wall apparently did not eliminate the exostome aril, the seed hairs, or the palisade layer.

The seeds of *Salomonia-Epirixanthes* have evolved similarly to those of the derived species of *Polygala.* The mesophyll is reduced, the palisade cells are well developed, the seeds are glabrous, and the seed appendages are very small. Wirz (1910) has already suggested that the absence of a thickened dermal apex in the outer integument of *Epirixanthes elongata* was responsible for the differences in seed form between this species and *E. cylindrica.*

Van Steenis (1968) suggested that the Australian *Comesperma* is linked with *Bredemeyera* through the New Guinean *B. papuana.* The latter lacks the coma and the exostome aril of the South American species but shares the isodiametric endotesta cells. *Bredemeyera papuana* has the same type of coma as *Comesperma* but lacks the firm cuticle and the tall palisade layer that adapt *Comesperma* seeds to life outside the rain forest. The similar tall palisade layer of *Polygala* and *Comesperma* apparently developed by convergent evolution. Although the differences in fruit morphology between *Comesperma* and *Bredemeyera* were disputed by Van Steenis, personal observation indicates that Rodrigue (1893) rightly pointed out that in both *Polygala* and *Bredemeyera-Comesperma* the development of a palisade layer is accompanied by the changeover from a fleshy fruit to a membranaceous capsule. Chalazal appendages are present in *Polygala* and *Bredemeyera* but attain their greatest development in the myrmecochorous species of *Comesperma.* Although the mode of dispersal of *Bredemeyera* has never been investigated, myrmecochory might represent a secondary development in *Comesperma,* as happened in many Australian plant groups (Berg, 1975). The present results support Van Steenis's hypothesis that the Australian *Comesperma* represents a derived branch of the South American *Bredemeyera,* which became adapted to subtropical drought conditions and assumed a virgate, microphyllous habitat.

GROUP 4 (fruits indehiscent, endotesta reduced; *Securidaca, Monnina*). This group is heterogeneous. In almost all species the protective function is completely taken over by the tough endocarp, which—unlike that occurring in the fruits of Group 1—consists of alternating layers of sclerenchymatic fibers (pers. obs.). At maturity the faintly developed endotesta reveals the polygalaceous nature of the seed coat, but in the two genera the testa reduction has followed two entirely different pathways.

In *Securidaca* ovule ontogeny is similar to that of *Carpolobia* and *Diclidanthera.* Due to different postfertilization development, major differences exist between the large seeds of the African species (*S. longepedunculata, S. welwitschii*) and the smaller seeds of the South American and Indo-Malesian representatives. The larger seeds contain an endotesta with cells slightly further differentiated than those of *Carpolobia*; the mesophyll and the glabrous epidermis are compressed. Because of an *Atroxima*-like postfertilization development, the seed contains a large, dorsal chalaza; the large investing embryo has thick cotyledons, the radicle is oriented toward the floral axis, and its almost globular shape allows expansion of the seed above the funicular attachment. In the smaller seeds of the other species, the testa is only weakly developed in the small, apical tegumentary portion of the pachychalazal seed (FIGURE 5F).

The presence of an endotesta and the *Atroxima*-like seed development in the African species suggest that these large seeds are primitive within the genus. In conjunction with the *Carpolobia*-like ovule ontogeny, this implies that *Securidaca* has evolved from a *Carpolobia*-like ancestor that became adapted to anemochory. The fruit of *Securidaca* lost its animal-attracting function and developed both a hard endocarp and an *Acer*-like samara, allowing for dynamic propulsion (Van der Pijl, 1982). The seed, in turn, lost its indumentum, and the mesophyll and the epidermis became compressed. In the smaller seeds the seed coat became further reduced by a pachychalazal development. Pachychalazy is mostly associated with large seeds, facilitating their vascularization (i.e., *Trichilia grandifolia*—Boesewinkel, 1981), and its function of eliminating the endotesta, as suggested here, has not previously been discussed.

In *Monnina* the incipient endotesta is disrupted, and only in some species do the cells thicken; then they are externally visible as brown spots dispersed over the glabrous seed. The disrupted endotesta of nonelongated cells, the dermalization of the outer integument, and the flat cotyledons with palisade parenchyma indicate a derivation from an ancestor with seeds borne in a bilocular capsule, conceivably resembling those of *Polygala* sect. *Hebecarpa* and *Bredemeyera.* This agrees with Wendt's (unpubl. ms) studies, which predict that the ancestor of *Monnina* must have had an unwinged bilocular fruit and would be classified as a *Polygala* if it had survived. With the development of the secondary closure of the capsule came an *Ulmus*-like fruit wing for gliding (Ulbrich, 1928) and a hard endocarp, which made the seed appendages and the testa redundant. Considering several floral characters and the similar fruit wing, Wendt (unpubl. ms) also suggested that *Monnina* might be related to *Polygala* sect. *Ligustrina,* but its seed anatomy is not compatible with such a derivation. Fruit wings probably developed independently in *Monnina* and in *Polygala.* Because of its giant fruit wing, *P. membranacea* has long been classified as a *Monnina,* but the seed has a well-developed testa and an aril (see Görts-van Rijn, 1974).

Hutchinson (1967) designated *Xanthophyllum* as the most primitive genus of the family, but this was criticized by Corner (1976) and Van der Meijden (1982). Although the seeds of *Xanthophyllum* were long believed to have only a reduced testa, this only holds true for the most derived infrageneric groups. The seeds of the most primitive infrageneric groups all have a subdermally initiated outer integument, thin cotyledons, a copious endosperm, a well-developed palisade layer, a thick mesophyll, radially elongated epidermal cells, and a glabrous seed with a solid hypostase (Verkerke, 1984). Compared with the seeds of Group 1 (*Carpolobia, Diclidanthera*), the most primitive *Xanthophyllum* seeds have two characters considered advanced within the family (the well-developed palisade layer and the glabrous seed), and in one species (*X. octandrum*) the orange to dark brown fruit is irregularly dehiscent. All other species have indehiscent fruits, and Van der Meijden (1982) considered the fruit dehiscence of *X. octandrum* to be a secondary development. The present results indicate that the fruit of *X. octandrum* can correctly be regarded as a locular dehiscent capsule, and that the elongated epidermal cells and the well-developed palisade layer are comparable to those of *Polygala membranacea* (Figure 1D). I have concluded that *Xanthophyllum* has evolved from a predecessor with dehiscent fruits, as must have happened with *Nylandtia* and *Epirixanthes,* and that the genus is not primitive within the family.

The results show that several evolutionary trends explain the great diversity in the fruits and seeds of the Polygalaceae, and that the evolution of seeds and fruits appears to be closely correlated. Complementary field observations of dispersal and germination could further enlarge our understanding of these evolutionary trends. The present results fit well with Wendt's (unpubl. ms) family cladogram but also indicate that old generic and tribal concepts may have to be changed in order to express the evolutionary relationships within the family.

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